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Erratum

The cut for Figs. 16–21, p. 499 was reversed in printing. Transpose 15 and 21; 16 and 20; 17 and 19.

STUDIES ON THE MORPHOLOGY OF THE ONAGRACEAE

VII. *Gayophytum ramosissimum*

DONALD A. JOHANSEN

(WITH PLATE 1 AND SIXTEEN TEXT FIGURES)

The phylogenetic position and relationships of *Gayophytum* have long been as obscure as those of many another genus in the Onagraceae. The most that has been conceded is that the genus is close to *Epilobium* (Trelease 1894, Johansen 1929); recently its position has been greatly clarified through the elucidation of its chromosome numbers. In the present paper, it is proposed to present an account of megagametogenesis and embryogenesis in a representative species, *G. ramosissimum* Torrey & Gray, and to make certain comparisons aimed toward defining the phylogenetic position of the genus.

The genus is very poorly known, owing to the small size of most of the species, the insignificant flowers and the restriction of the various species in both North and South America to comparatively inaccessible portions of the high mountains. Extremely little has been contributed to our knowledge of the genus, or of any of its species, since Trelease's revision (1894). Most accounts which have appeared in the meantime, particularly those in floras, are drawn wholly from this source.

Gayophytum is represented in western North America by about nine species, with others in western South America. No species seems to be known from either Mexico or Central America: the reason for this gap needs to be explained by future monographers of the genus.

MATERIALS

Gayophytum ramosissimum is a widespread form, occurring from Washington easterly to Montana, thence south to Colorado and through Nevada and Arizona to California and down into Baja California as far as the Sierra San Pedro Martir. It does not seem to be known from Oregon. Material of no other species has thus far been procurable, hence it will be necessary to consider *G. ramosissimum* as typical of the genus in so far as phylogenetic considerations are concerned.

Two different collections from widely separated localities have been available for study. One lot was collected by Dr. Ira L. Wiggins on September 2, 1927 in open flats in a pine forest, at an altitude of about 6100 ft., in the Laguna Mts. of San Diego County, California. The other collection was secured by the writer on September 6, 1930 from plants growing along the roadside in a pine forest near the summit of Donner Pass in the Sierra

Nevada Mts. of Nevada County, California, at an elevation of 7135 ft. *G. ramosissimum* is essentially a high-montane species, but is not an alpine plant. The two groups of material are identical morphologically and cytologically, hence in the descriptions and figures no distinction is being made.

The material collected by Dr. Wiggins was thoroughly studied during the same year that it was collected but not all stages were represented, and it was therefore necessary to postpone the completion of the study until the second lot of material was available.

OVARY AND OVULES

The ovaries of *G. ramosissimum* resemble those of that group in the genus *Epilobium* represented by *E. paniculatum* but are biloculate and the number of ovules to each loculus averages six. The ovules regularly alternate in the adjoining locules.

The ovules are rather small, as are the mature seeds. The nucellus is of slight extent; although not attacked to any appreciable extent by the developing megagametophyte, it nevertheless has completely disappeared by the time the embryo has completed growth. Both a hypostase and an epistase are present; the latter originates almost simultaneously with fertilization, hence appears far earlier than it does in any other onagrad known to us.

In practically every older ovary there are generally to be found quite a few aborted ovules. The sterility of these ovules seems to be due to only two causes. One is the failure of the functioning megaspore to continue growth once it becomes started. This phenomenon has been observed repeatedly. The other cause is a unique one: after the second division in the young megagametophyte, the three upper groups of chromosomes, which should form the egg nucleus and synergid nuclei respectively, are unable to reconstitute themselves into nuclei but become clumped together and finally break down completely (Pl. 1, fig. 15). This phenomenon, when first noticed, was naturally thought to be evidence of poor fixation, but careful study of a large number of cases at all stages finally revealed the true explanation. We had previously observed the same thing in other genera (e.g., *Taraxia ovata*, *Zauschneria latifolia*, etc.) but were not then aware that it was of any significance as a cause of ovular sterility.

MEGAGAMETOGENESIS

The megagametophyte originates in the fashion typical for the family, and its growth into the quartet is likewise typical. In the Donner Pass material we frequently found metaphases and anaphases of the first division, but the excessively small size of the chromosomes precluded, in

most cases, the making of accurate counts. In Plate 1, fig. 1, is shown a clear diaphase figure with eleven bivalents. The extremely small size of the anaphase chromosomes can be seen in Plate 1, fig. 2. Here, too, there are eleven elements and the split for the second division is already evident. The chromosomes preserve their identity during the interphase (Pl. 1, fig. 3); several such stages have been encountered and in most of them it was possible to count eleven chromatin blobs which were distinctly constricted in the center, exactly as in the anaphase figure.

The micropylar megaspore of the quartet (Pl. 1, fig. 4) is always the functional one (Pl. 1, figs. 5, 6).

The plane of the first division in the young megagametophyte is either transversely or longitudinally situated; the latter position is the normal one among onagrads. There seems to be some evidence that the nuclei resulting from a transversely placed division figure do not later become oriented one above the other, as not infrequently happens in other onagrads, but divide while still in the positions first assumed, and the spindles of the second division are irregularly oriented as a consequence. In this probably lies the explanation of the erratic organization of many megagametophytes.

The mature megagametophyte most commonly observed is similar to the one portrayed in Plate 1, fig. 9. This type plainly shows the effects of an inadequate water supply. A well organized megagametophyte is not often found (Pl. 1, fig. 10); the synergids are well indented and each possesses a rather fragile so-called filiform apparatus that easily collapses and disappears. The egg cell is comparatively small and the polar nucleus is much less prominent than in other onagrads. In many well nourished megagametophytes the synergids and egg cells contain much starch, and in some embryo sacs which were especially well nourished, the megagametophytes were heavily gorged with starch grains of a large size.

FERTILIZATION

All the stages of syngamy, as well as the fusion of the secondary male nucleus with the polar nucleus, have been observed. The entire process in each union does not differ in any manner from the descriptions for other species already presented. Plate 1, fig. 11, shows a stage rarely found, and it is one which we have hitherto not been able to figure. The primary male nucleus is in the very act of entering the neck of the egg cell, while the secondary male nucleus is in the megagametophytic cytoplasm (to the left of the egg cell), on the way down to meet the polar nucleus. Plate 1, fig. 13, shows a middle stage of syngamy, while figure 14 shows a corresponding stage in the union of the secondary male nucleus with the polar nucleus.

During fertilization there can sometimes be found in the upper part of the embryo sac many globular bodies having the staining reaction of chromatin; they are similar to those described in *Zauschneria latifolia* (Johansen, 1931), but we could not ascertain anything about their origin.

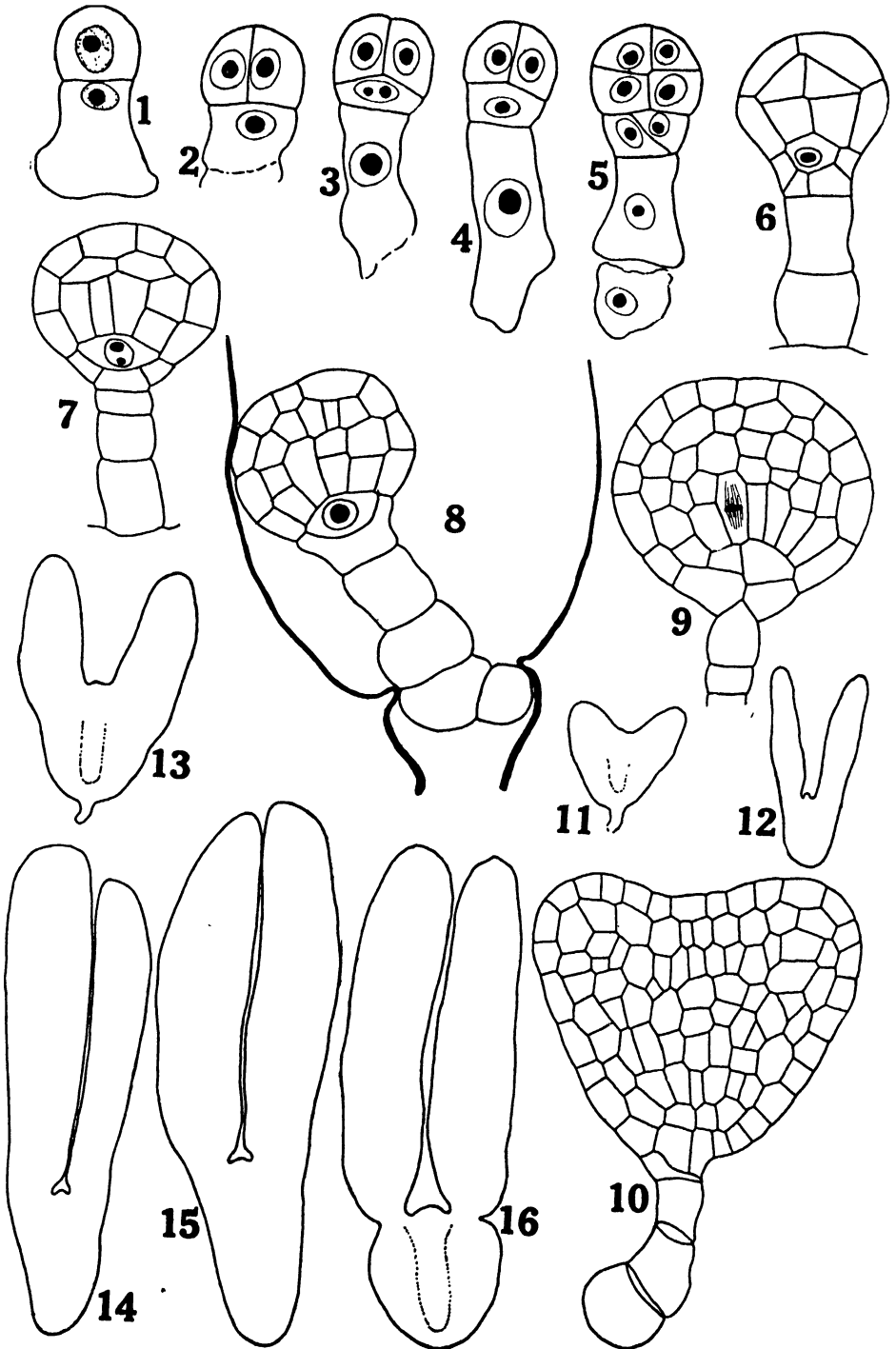
EMBRYOGENESIS

For some obscure reason, the zygote delays division for a long time. The earlier divisions are typical (text figs. 1-4). The suspensor initial cell may become much elongated (fig. 4) before it is transversely split into two or more unequal cells (figs. 5-7). The suspensor of this species is, in fact, far more persistent despite its small size than in the species in other genera which have suspensors of similar size and construction. It has even been observed to grow out into the tapetal portion of the ovule (into the channel left by the microgametophyte) and to become wedged in the opening in such a manner that the young embryo literally appears as if suspended in the embryo sac by its suspensor (fig. 8).

The hypophysis cell in *G. ramosissimum* behaves rather inconsistently, and it is for this reason that the radicle cannot always be clearly delimited in mature embryos. An examination and comparison of figures 5-9 will bring out this point. In figure 5 an oblique wall divides the hypophysis initial; a second oblique wall will presently be formed in the cell to the right and by a division in the cell at the left this wall will apparently be continued through to the opposite outer wall. Figure 6 shows the result of this method of origin of the root-tip (still only one cell in extent) and the root-cap. In figure 7 we have the usual representation of the earlier divisions in the hypophysis initial. In figure 8 the hypophysis cell has divided in the characteristic manner but no walls have yet been erected in the lower cell, which gives rise to the root-cap tissues.

The later developmental stages are wholly typical. Mature embryos are almost exact duplicates of the normal embryos (*Type A* embryos) of *Zauschneria latifolia*; e.g., compare figures 14-16 of this paper with figures 67-69 of the latter species in a former paper (Johansen 1931). In the oldest embryos, organization of the various tissues is the most regular and symmetrical that we have yet encountered in the Onagraceae.

Figs. 1-16. Embryogenesis. Except where noted, the magnification is 950. 1. Two-celled stage. 2. Three-celled. 3. Quadrant stage. 4. Quadrant with elongated suspensor cell. 5. Octant. Notice oblique division in hypophysis cell. 6, 7. Later stages. 8. Embryo whose suspensor has grown into the channel left by the microgametophyte. As the embryo actually hangs downward in nature, the figure should be reversed for a more accurate conception of its position. 9. Globular stage. 10. Beginning of cotyledon development $\times 475$. 11-13. Stages in cotyledon development. $\times 120$. 14-16. Latest stages in development. $\times 120$.



ENDOSPERM

The polar nucleus takes up a position at the center of the embryo sac (Pl. 1, figs. 9–10). Following the first division after fusion with the secondary male nucleus, the two resultant nuclei remain at the center but not close together. After the second division, two nuclei remain at the center, while one nucleus moves to the vicinity of the egg cell and the fourth goes to the extreme chalazal end of the embryo sac, as shown in Plate 1, fig. 12. Later divisions were not followed out.

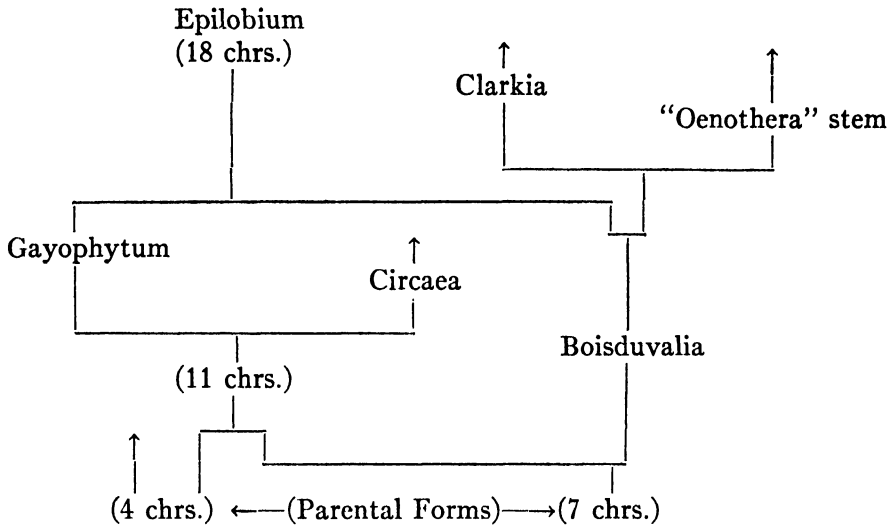
The “endosperm” nuclei rarely total over twenty and all vestiges have disappeared by the time the embryo approaches maturity.

The division figures in the “endosperm” are exceptionally clear in *G. ramosissimum*. Mitoses are generally simultaneous in any given ovule, while in the majority of other genera they commence at the micropylar end of the sac, progressing towards the opposite end. Many counts have been made and the number (diploid) was always 22.

THE PHYLOGENETIC POSITION OF *GAYOPHYTUM*

As explained in the opening paragraph, *Gayophytum* is taxonomically most closely related to *Epilobium*. The cytological evidence of the relationship, however, is at first contradictory because the basic number of chromosomes in the one is 11 and in the other 18. It has already been suggested that *Epilobium* should be considered as of hybrid ancestry (Johansen 1929), but until now the position of *Gayophytum*, whether above or below *Epilobium*, has remained doubtful. Recalling that the family presumably originated from two forms, one of which possessed $4n$ chromosomes, the other $7n$, and that a cross between the two parental forms would reasonably have $11n$ chromosomes, we immediately obtain a good basis for speculation. Genetical studies on other plants have previously shown that the result when a cross is in one direction is not always the same when the cross is reciprocal. We are evidently dealing with a similar cross here, since we already have a series in which the basic number of chromosomes is 11 (*Circaea*, *Lopezia*, *Fuchsia*, etc.) but to which *Gayophytum* shows no systematic relationship. From the crosses between the two parental forms, in other words, two phylogenetic lines arose. One of these begins with *Gayophytum* and, so far as our present knowledge goes, also stops there. To complete the chain of evidence placing *Gayophytum* below *Epilobium* phylogenetically and to demonstrate further that the former is one of the parents of the latter, we have but to find the other presumable parent of *Epilobium*. Certain taxonomists have expressed a mild opinion that some sort of relationship exists between *Epilobium* and *Boisduvalia*. (The latter genus is directly derived from the $7n$ chromosomal ancestor.)

To sum up a strong probability, *Epilobium* represents a hybrid between *Gayophytum* and *Boisduvalia*. A diagrammatic representation of the idea may assist in making it clearer:



It might be profitable to examine some of the evidence underlying the assumption outlined above. First, the cytological evidence is in agreement, and incidentally all three genera concerned have very tiny chromosomes. Second, there is considerable morphological evidence, much of which has not yet been published. It is unfortunate that the few accounts of the embryology of *Epilobium* are so fragmentary as to be valueless. The writer's own investigations on several species in this genus reveal that embryogenesis differs greatly among different species; that is, there are so many divergencies in various details that a single description will hardly cover the entire genus. The embryos of *E. californicum* and *E. lanceolatum*, for example, differ much in size and in the latter species the behavior of the hypophysis cell is peculiar. Nothing has been published on *Boisduvalia*, but *B. campestris* and *B. densiflora* have been studied to some extent. Sufficient is known of the embryology in all three genera, in any event, to warrant the statement that the embryology of *Epilobium* is essentially a fusion of that of *Gayophytum* and *Boisduvalia*, some species resembling peculiarities in one of the latter genera, others those of still other species.

SUMMARY

1. The phylogenetic position of *Gayophytum* has been so obscure that an attempt was made to solve the problem on the basis of cyto-morphological data.

2. In the representative species studied, *G. ramosissimum*, the ovaries are biloculate, with an average of six ovules to each loculus.
3. The nucellus is of slight extent and disappears early during growth of the embryo.
4. Two causes of ovular sterility are described.
5. Megagametogenesis is typical; the micropylar megaspore is the functional one.
6. The embryology is fairly regular. No apomictic structures have been encountered.
7. The chromosome numbers are $n=11$, $2n=22$. These indicate that the genus arose as a cross between the two parental forms of the family.
8. *Gayophytum* is one parental form of the hybrid genus *Epilobium*, the other presumably being *Boisduvalia*.

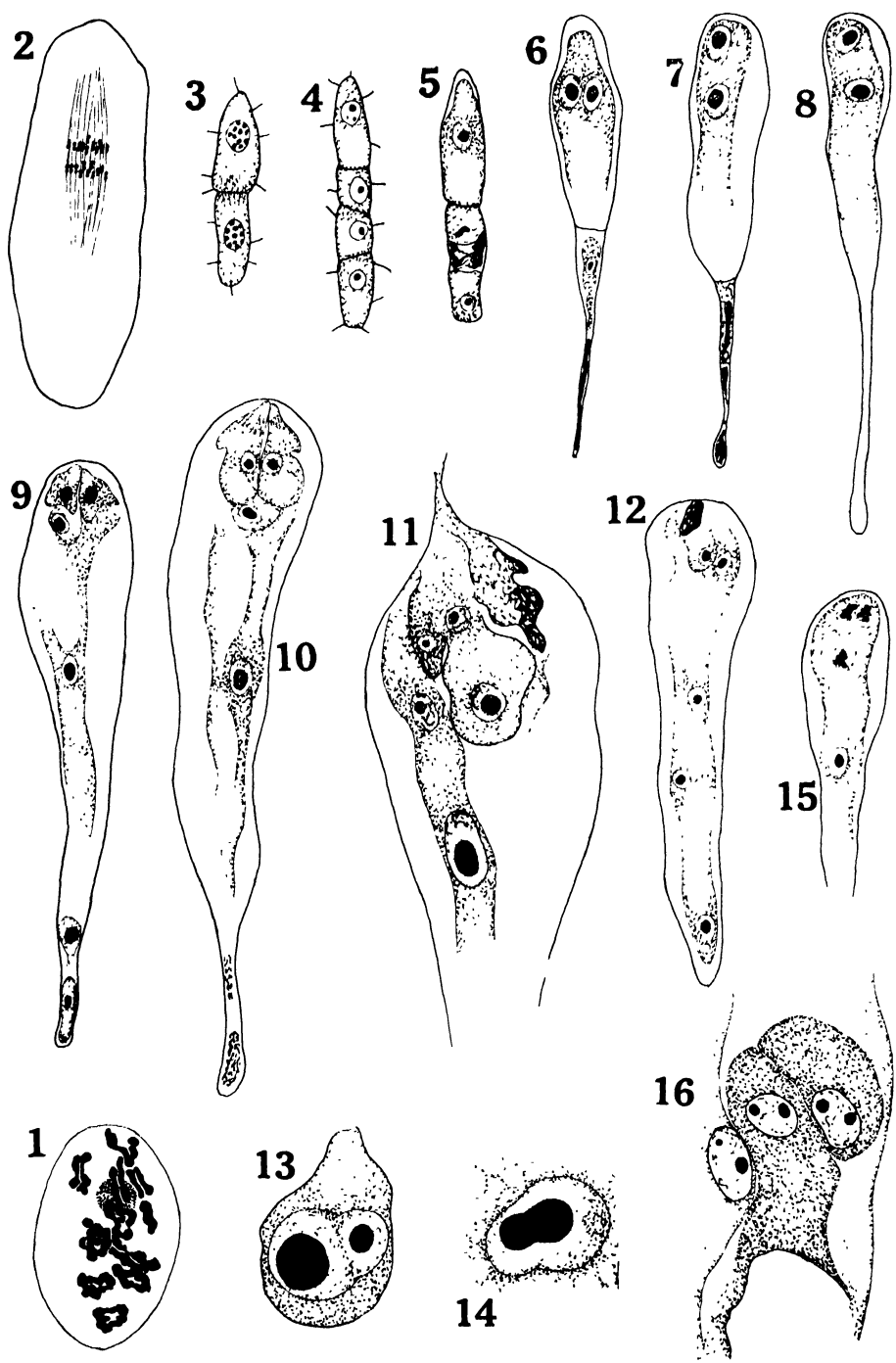
The greater part of this study was prosecuted during the tenure of a National Research Council Fellowship in the Biological Sciences, with residence at Stanford University.

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- . 1931. Studies . . . V. *Zauschneria latifolia*, typical of a genus characterized by irregular embryology. *Ann. New York Acad. Sci.* **33**: 1-26.
- Trelease, W. 1894. Revision of the North American species of *Gayophytum* and *Boisduvalia*. *Ann. Rep. Missouri Bot. Gard.* **5**: 107-122.

Explanation of plate 1

Figs. 1-16. 1. Diaphase from megasporocyte, eleven bivalents. $\times 1250$. 2. Anaphase of first division in megasporocyte. $\times 475$. 3. Interphase. $\times 475$. 4. The quartet. $\times 475$. 5. Beginning of growth in the functioning megaspore. $\times 475$. 6-8. Binucleate megagametophyte, the first figure with the nuclei oriented side by side, the other two with these nuclei one above the other (normal position). $\times 475$. 9. Type of mature megagametophyte usually found. $\times 475$. 10. Well nourished megagametophyte, showing regular organization. $\times 475$. 11. Fertilization. Primary male nucleus in neck of egg cell; secondary male nucleus to right of egg cell. One synergid nucleus is between the two male nuclei. $\times 950$. 12. Disposition of "endosperm" nuclei after second mitosis. Zygote shows no sign of approaching division. $\times 475$. 13. Syngamy. $\times 1250$. 14. Fusion of secondary male nucleus with polar nucleus. $\times 1250$. 15. Typical instance where nuclei were not organized at micropylar end of megagametophyte after second division in latter. $\times 950$. 16. False "embryo" in endosperm; it had six "cells" altogether. $\times 1250$.



Crown gall on Sahuaro (*Carnegiea gigantea*)¹

MICHAEL LEVINE²

(WITH PLATES 2, 3)

Up to the present time the crown gall disease has been unknown on any member of the Cactaceae. Smith (1911) reported the effects of inoculation of a poplar strain of *Bacterium tumefaciens* on four varieties of *Opuntia*. In only one case was a small "tumor" formed four months after inoculation which regressed eight months afterwards. No sections of this material were reported. The so-called grape strain of *B. tumefaciens* gave no results when the *Opuntia* was inoculated with it. It appears that up to the present, no complete evidence has been presented to show that the Cactaceae react to the crown gall organism.

Smith (1922) contended further, that fasciations can be produced in *Nicotiana*, *Pelargonium*, *Ricinus*, *Brassica*, and *Tropaeolum* by inoculations with *B. tumefaciens*. Fasciations, he believed, result from disturbances due to the penetration of a foreign organism into the growing point. This causes crowding and division of the growing point or brings about irritations which lead to fusions. Shreve (1931) believes that fasciations in cacti, "cristates" as they are called, are not the results of fungi or bacteria but are probably due to a mechanical injury induced by a foreign substance introduced by an insect. *B. tumefaciens* or strains of this organism have not been isolated from the cacti. The existence of cristates suggests such a possibility and further study on these structures is needed.

The importance of having material for crown gall study available at all times has led me to investigate a number of species of *Opuntia*. The common house and garden plants commonly used in laboratories for crown gall studies, require much attention. They grow old, woody, shed their leaves, and become quiescent after they are transferred from the garden to the laboratory, which makes them unavailable subjects of experimentation for a number of months. The other disadvantage in the use of the ordinary plants lies in the rapid development of the tumor so that the progress of the growth cannot be studied with great detail. The cacti so far studied are not suitable for testing the virulence of various strains of *B. tumefaciens* because of the slow development of the tumor.

It is generally accepted in all tumor work, animal and plant, that the younger the host the more rapid is the response and the greater is the development of the new growth. From this point of view, it appeared to be

¹ Completion made possible by a grant-in-aid from the Chemical Foundation.

² Laboratory Division, Montefiore Hospital, N. Y.

of interest to determine what happens to the Sahuaro when subjected to an inoculation with a virulent strain of *B. tumefaciens*. MacDougal (1926) pointed out that the cells of the Sahuaro show individual activity for periods over a century. This view is apparently correct for the study reported below shows comparatively old cells capable of producing neoplastic responses which have not been obtained in tissues of other plants of similar or younger age. Then again, it is of importance to determine, in view of the reported long period of individual activity of these cells, whether or not the new formation on this tree-cactus would behave like the galls on other plants. The observations of the present writer (Levine, 1931) led him to the conclusion that the cells of the crown gall tissue are at first embryonic in nature but soon become differentiated, mature, and die. It was of interest to study the behavior of the cells in Sahuaro tumors.

Without resorting to field material it is impossible to inoculate the very old tree-cacti, but by inoculating the side ridges of small Sahuaros, approximately five to six years of age, it is possible to study the reaction of much older tissue than one can obtain by inoculating the growing shoots of the leafy plants generally used for crown gall study. The age of the growing shoots of the latter may be but a few days to a week old, while the cells along the ridges of the Sahuaro may be over a year old. According to Britton and Rose (1920, p. 164) Shreve states that the Sahuaro, at the age of eight to ten years, is only four inches tall. It is estimated (Shreve, 1931) that the rate of growth in larger plants is about four inches a year. Growth in these young plants is very slight, so that at the age of thirty years they are only three feet tall.

MATERIAL AND METHODS

In the fall of 1926 a large number of young joints of *Opuntia* were sent to me through the courtesy of Dr. D. T. MacDougal from southern United States, Mexico, and South America. A collection of joints³ already rooted, were furnished me by the New York Botanical Garden. These plants were set out under favorable conditions in the laboratory where an abundance of sunlight was present for the major portion of the day. In April, 1931, a dozen Sahuaro plants from Arizona were sent to me by Dr. MacDougal. These were wrapped in cotton and were somewhat shriveled when they reached New York. These plants were potted and set out in the greenhouse under favorable conditions until they struck roots.

Some *Opuntia* joints were cut aseptically and placed in large sterile culture dishes and then inoculated by covering one cut surface with one of

³ *Opuntia Keyensis*, *O. Dillenii*, *O. stricta* and *O. Linderheimeri* were furnished me through the courtesy of Dr. N. L. Britton, to whom I owe my sincere thanks.

two strains of *B. tumefaciens*, used at that time in my laboratory. The rooted plants were inoculated in the usual way. Tumor tissue which developed was removed from the plant without disturbing the rest of the growth, while in other instances, a longitudinal section was made to pass through the medium portion of the gall and the plant. Sections of the tumor tissue including normal parts of the plant, were fixed in Bouin's and Flemming's weaker solutions. The material was imbedded in paraffin and serial sections 7.5μ to 10μ in thickness were cut. These were stained in Flemming's triple stain or in Heidenhain's iron haematoxylin.

OBSERVATIONS

The Opuntia

The Opuntia, as well as the Sahuaro, when inoculated with a virulent strain of *B. tumefaciens* produces first, an area of necrosis. This area, it would seem, is most apparent in plants that respond slowly to the inoculation of the bacteria. This necrotic area is also present in the sections of joints prepared in culture dishes. No reaction followed in these sections for a period of over three months. Then however, the pieces of the cactus began to disintegrate and became invaded by moulds. No reactions were found similar to those reported by Smith (1911) for sections of turnips or Blumenthal and Hirschfeld (1917), and Magnus (1918) for sections of carrots. The rooted joints of the Opuntias, in most cases, produce comparatively large areas of necrosis which become progressively brown and then black in color and finally harden, leaving a small depression in the region of inoculation. Sections through these areas show compact tissue below the necrotic area in the nature of a callus. Invariably, these sections show invasion of hyphal strands. In no instance was a well-formed tumor mass formed on the Opuntias studied, yet new joints were formed by tissues adjacent to the region of inoculation.

The Sahuaro crown gall

Tumors on the Sahuaro are formed after inoculation with a virulent strain of *B. tumefaciens*, introduced into the tissue by the aid of several pricks of a needle which had been previously immersed in a sub-culture of the organism. As in the Opuntias, the first reaction to the inoculation is the formation of a small blackened area around the needle pricks. This, it would seem, is due to the destruction and death of the seriously injured cells. The development of the tumor tissue in this cactus is relatively of long duration as compared with the reaction of the common plants generally used for the experimental study of this type of tumor. The necrotic areas induced in these plants persist for a long time also. In such plants

as the tomato, sunflower and the castor bean, the necrotic area persists for a short time and new formations may be detected in actively growing plants within a few days. I have studied sections of the early stages in tumor formation in connection with another problem which is under investigation, and found active cell proliferation in the tomato and sunflower within two to three days after inoculation.

In the Sahuaro the necrotic area persists for over a month or more, but is soon followed by the development of small pale-green modules on one side of the destroyed tissue; or they may arise from cells below the dead tissue. Two or several coalescing nodules may form simultaneously at the region of inoculation. The nodules are very small at first, but grow comparatively fast. The first photograph of these nodules was made six months after inoculation. An average tumor at this age is shown in figure 1. The largest gall formed is approximately 15 mm while the smallest is about 3 mm to 4 mm through its largest diameter. A tumor eleven months old is shown in figure 2. Fourteen months after inoculation, the largest gall measured 2 cm to 3 cm as shown in figures 3 and 4. It must be borne in mind that the tallest Sahuaro in my collection at this time, measures 8 cm to 10 cm above the soil.

These tumors on the Sahuaro are old galls chronologically when compared with tumors on the other flowering plants generally used for this study. Yet they are soft and section readily as pointed out below. A well-formed gall on the rubber tree, *Bryophyllum* or any other perennial plant so far studied, is filled with whorls of woody tissue and cork, making a microscopic study of this tissue by the usual means, impracticable.

The tumors on the Sahuaro, as those on other plants, are smooth and resemble more closely tumors found on the garden beet, *Beta vulgaris*. They are usually sessile and surrounded by host tissues, as shown in figure 4; or they may have a short, thick stalk, as shown in figure 3. In this figure it is of interest to note that a layer of epidermis has formed on one side of the gall containing a large number of densely set areoles with numerous spines. This would be comparable to the leafy shoots frequently found on galls of tobacco, and less commonly on the geranium and Jimson weed (*Datura stramonium*).

Histology of the Sahuaro tumor

Nodules of several tumors were studied in long serial sections. As noted above, the tumors fix readily in Bouin's and Flemming's weaker solution and present beautiful sections for microscopic study when stained with Flemming's triple mixture. Large pieces of the tumor tissue were prepared so as to give a complete picture of the histology of the tumor.

The tumor tissue is made up of parenchymatous cells interspersed with numerous areas of more actively growing, undifferentiated cells. Whorls of cells composed of protoxylem with well-formed tracheids are abundant.

In a section of a young nodule such as that shown in figure 6, two distinct areas may be observed; the peripheral portion, which is made up of small embryonic-like cells, and the larger interior portion, made up of larger and maturer cells. Figure 6 represents a longitudinal section through one of the nodules shown in figure 2. The surface or periphery of the small tumor mass consists of several layers of embryonic-like cells mentioned above. These cells show a comparatively large nucleus imbedded in a homogeneous densely granular cytoplasm. No evidence of an epidermis and palisaded layers of cells is present. Necrotic cells are found adhering to the surface of the peripheral layer of the tumor. The interior parenchymatous cells are of various sizes, due probably to sections of these cells whose polarity has been disoriented. The cytoplasm of the parenchymatous cells consists of a coarse reticulum made up of extremely fine granules as shown by MacDougal (1926). In sections of larger tumors, such as shown in figure 4, abundant clusters of protoxylem cells appear in the tissue, as shown in figure 7. They consist of elongated, cylindrical cells with small nuclei and dense cytoplasmic material. In some sections of this tissue, spiral tracheids may be seen in the process of development.

I have been unable to find early stages in nuclear division in the peripheral or parenchymatous cells of this tissue. Chromosome counts of the cells of this tumor would be of great interest. Late stages of nuclear and cell divisions are common, however. In the older cells, starch grains are abundant while in the young cells, such as shown in figure 6, they are entirely absent.

I have studied the slime or mucilage cells in the host tissue and searched the tumor material for similar structures. In none of my tumor tissue on this plant have I been able to find evidence of the presence of these cells. The mucilage cells, while not present in the tumor tissue, appear to be more abundant in the host tissue adjacent to the tumor. Figure 8 is a section through a gall shown in figure 4. The photograph represents the area of the tissue lying between the host and gall tissue. The area to the upper right in the figure represents gall tissue. The rest of the figure represents host tissue. The host tissue is characterized by a large number of the mucilage cells which are evidently very abundant below the base of the tumor tissue. The presence of these cells, it seems, may also serve as a defense mechanism. It appears that the injury which induced the crown gall tissue may have indirectly stimulated the formation of a larger number of slime cells than usual. The absence of these cells in the crown

gall tissue may be associated with the age of the gall. It is possible that in still older neoplasms of the Sahuaro, mucilage cells may be found. Sections of normal portions of the tree-cactus show a preponderance of mucilage cells forming a zone below the palisade layer, while they are less frequent in number towards the middle portion of the plant.

The mucilage cells of the Sahuaro are larger than the cortical cells of this plant. Frequently, two or more cells seem to fuse, forming a large mass of mucilage as shown in the upper left of figure 8. This may have led to the idea that mucilage forms in inter-cellular spaces as maintained by earlier workers. My observations of the formation of mucilage cells lead me to concur with the views of Miss Stewart (1919) that the slime and mucilage cells are a product of the cytoplasm and nucleus. As the slime increases in the cell, the cytoplasm and nucleus are crowded into a smaller space until the protoplasm of the cell completely disappears. My figures of old mucilage cells show rather constantly the presence of a diffusible substance on the periphery of the mucilage cell which permeates the surrounding cells. The substance stains a deeper gentian violet than the stratified mucilage, as shown in figure 9. The significance of this zone about the mucilage cell is not clear.

I wish to express my sincere thanks to Doctor D. T. MacDougal, who through a period of six years, has furnished me with various species of cacti and whose advice has been a great stimulus to me.

SUMMARY

1. As far as the crown gall literature is available, it appears that crown gall disease on the Sahuaro (*Carnegiea gigantea*) is reported here for the first time.
2. The tumors on this plant were induced by inoculations with *B. tumefaciens*.
3. Sections of these growths show structures which are analogous to crown gall tissue on other flowering plants studied.
4. The tumors on the plants reported here are the oldest (chronologically) crown gall tissues so far studied microscopically.

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Explanation of plates 2, 3

The photomicrographs were made with Zeiss 35 cm. camera.

Fig. 6 was made with the aid of Zeiss Obj. 6 and oc. K 3 bellows 25 cm.

Figs. 7-9 were made with the aid of Zeiss Obj. 10 and oc. K 10 bellows 25 cm.

Fig. 8 was made with the aid of Zeiss microplanar 3.5 cm. and bellows 50 cm.

Fig. 1. Sahuaro inoculated with *B. tumefaciens* 6/13/31, photographed 12/13/31 showing small tumor at point of inoculation. $\times 1/2$.

Fig. 2. Another plant showing three fused tumor masses eleven months after inoculation. $\times 2.3$.

Fig. 3. Smooth globular tumor with clusters of areoles and spines 13 months after-inoculation. $\times 1$.

Fig. 4. Rough warty crown gall showing necrotic area.

Fig. 5. Longitudinal section of the plant shown in fig. 4. Note attachment of sessile tumor.

Fig. 6. Longitudinal section of the nodule of the tumor shown in fig. 2. Note small size of peripheral cells; no mucilage cells.

Fig. 7. Section of tumor showing protoxylem cells.

Fig. 8. Longitudinal section through tumor shown in figs. 4-5. Note distribution of mucilage cells below base of tumor in a region distinctly host tissue.

Fig. 9. Enlarged portion of a section of fig. 7. Note the halo of the diffusible substance about the mucilage cell.



LEVINE CROWN GALL



LEVINE CROWN GALL

Asterohyptis: a newly proposed genus of Mexico and Central America.

CARL EPLING

(WITH TEXT FIGURE)

Asterohyptis gen. nov.

Suffrutices ramosi ramulis gracilibus divaricato-ascendentibus; foliorum laminis nunc ovatis nunc lanceolatis sat magnis sat tenuibus, breviter petiolatis; floribus in cymulis densis in foliorum valde diminutorum axillis sessilibus, glomerulis globosis maximam partem spicas interruptas moniliformes formantibus rarius in spicas densas cylindratas congestis, bracteis lineari-setaceis brevibus subtentis; calycum florentium tubis campanulatis 10-venis, ore truncato nunc nudo nunc hirsuto, dentibus subulatis, nunc leniter recurvis nunc valde stellato-patentibus subaequilongis, in maturitate tubis paulo auctis cylindratis, dentibus fere immutatis; corollarum tubis cylindratis, superne leniter ampliatis intus hirtellis, laciniis subrotundis *subaequalibus lenissime bilabiatis*, labiae inferioris lacinia media leniter concava integra, in basi nullo modo angustata *nec in rugam contracta*; staminibus quatuor didymis, duobus posticis brevioribus saepius in tubo inclusis anticis e tubo breviter exsertis, omnibus *lenissime* declinatis; stylo breviter exserto ramis brevibus obovatis subplanis; gynobasis columella quam ovulis brevior; nuculis ovatis leniter complanatis minutissime punctato-rugosis.

Asterohyptis per *Hyptidem stellulata*, *H. Mocinianam* et *H. Seemannii* constituta est; species typicam *A. stellulata* designo.

Glomerula in maturitate 8–12 mm. diametro; calycum dentes 1.5–3.5 mm. longi.

Calycum florentium tubi 1.5–2 mm. longi, dentes
maximam partem 1.5–2.5 mm. longi, in maturitate
tubi 2.5–3.5 mm. longi; inflorescentia matura
moniliforma

1. *A. stellulata*

Calycum florentium tubi 1.2–1.5 mm. longi, dentes
2.5–3.5 mm. longi, in maturitate tubi 1.5–2 mm.
longi; glomerula matura saepius in spicas
cylindratas conferta

2. *A. Mociniana*

Glomerula in maturitate 5–7 mm. diametro; calycum dentes .5–.7 mm. longi.

3. *A. Seemannii*

1. *A. stellulata* comb. nov.

Hyptis stellulata Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr. 12:128.1848 per specim. in Mexico prov. Morelos prope Cuernavaca a Berlandier lectum constituta est; typum in herb. Kew., isotypos in herb. Mus. Brit., Berolin., Gray. et Vindob. vidi.

H. pubescens Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr.

12:128.1848 per specim. in Mexico a Moçino et Sesse lectum constituta est; typum verisimiliter verum e herb. Lambertiano in herb. Kew., isotypos probabiles in herb. Mus. Brit. vidi. *Mesosphaerum stellatum* et *pubescens* Kuntze, Rev. Gen. 2:526, 527.1891 (nomina).

Suffrutex aromaticus altitudine 1–3 m. ramulis gracilibus divaricato-ascendentibus obtuse quadratis sulcatis, pilis brevibus nunc extensis nunc ascendentibus vestitis, internodiis 3–8 cm. longis; foliorum laminis maximam partem anguste ovatis, 3–8 cm. longis, 1.5–3.5 cm. latis, acutis, in basi nunc rotundato-truncatis nunc rotundato-angustatis, margine subdupliciter serrulata, crenis ad 1.5 mm. altis, pagina superiore viride hirtella, inferiore villosula etiam subtomentosa pallidiore etiam incana, petiolis ad 1.5 cm. longis

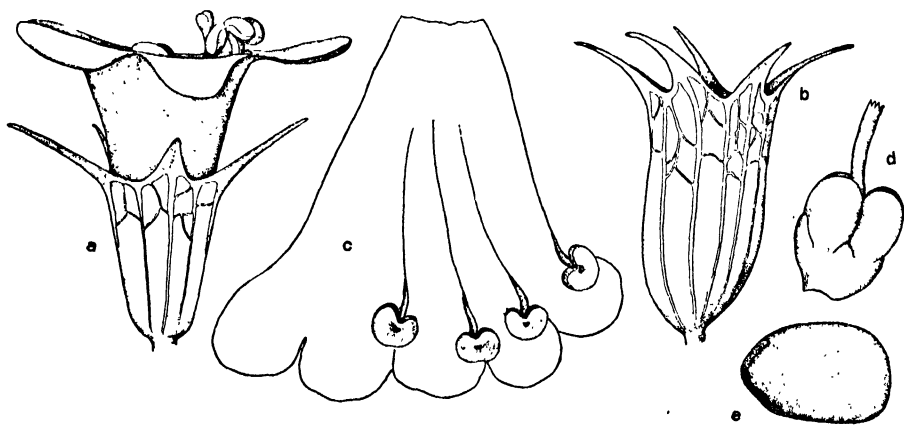


Fig. 1. *Asterohyptis stellata*. a, flower; b, mature calyx; c, corolla split open; d, ovules and gynobase; e, nutlet.

elatis; verticillastris in maturitate 8–12 mm. diametro, rarius in spicas cylindrates densas confertis; calycum florentium tubo 1.5–2 mm. longo, dentibus 1.5 interdum 2.5 mm. longis saepius utrinque hirtellis, in maturitate tubo 2.5–3.5 mm. longo; corollarum tubo 1.5–2 mm. longo; nuculis 1–1.2 mm. longis.

Mexico: **Sonora**: in Sierra de los Alamos, 17.IV.1910, *Rose 12995*; **Sinaloa**: prope Balboa, I.1923, *Ortega 4985*; San Ignacio, 500 m., 9.III.1918, *Montes 265*; **Nayarit**: inter San Blas et Tepic, *Sinclair*; prope Acaponeta, 25. II.1927, *Jones 23154*; prope Acaponeta, 1.III.1927, *Jones 23152*; La Barranca, 21.II.1927, *Jones 23153*; prope Tepic, 9–10.II.1927, *Jones 23257*, 23151; prope Tepic, I–II.1892, *Palmer*; prope Ocotillo, 28.V.1849, *Gregg 958*; prope Tepic, II.1895, *Lamb. 523*; prope Acaponeta, 10.IV.1910, *Rose 14301*; **Durango**: Chocala, 5.III.1899, *Goldman 349*; **Zacatecas**: sine loco, *Hartweg 172*; **Aguas Calientes**: sine loco, *Hartweg 172*; **Jalisco**: sine loco, *Beechey*; Etzatlan, 5.X.1908, *Barnes et Land 242*; prope Guadalajara, 5000 ped., 6.X.1903, *Pringle 11677*; prope Guadalajara, 5000 ped., 9.X.1903, *Pringle 11676*; prope Tuxpan, II.1904, *Purpus 500*; in Cerro de Ameca, XII.1899, *Diguet*; in Barranca del Rio Santiago, X.1899, *Diguet*; prope Guadalajara, 22.X.

1889, *Pringle* 2727; ad Rio Blanco, 1886, *Palmer* 326; prope Magdalena, 24.V. 1849, *Gregg* 882; inter Huejilla et Mesquitec, 25.VIII.1897, *Rose* 2563; **Colima**: sine loco, 1891, *Palmer* 1203; **Michoacan**: Morelia, Loma Sta. Maria, 26.VIII. 1909, *Fr. Arsène* 2971; El Ocote, 500 m., 2.XI.1898, *Langlasse* 690; **Morelos**: prope Cuernavaca, 12–14.XI.1865, *Bourgeau* 1277; prope Cuernavaca, 20.X.1827, *Berlandier* 1058 T, 959; prope Cuernavaca, 31.VIII.1910, *Orcutt* 3894; prope Yautepec, 4000 ped., *Pringle* 11100; in collibus prope Cuernavaca, 5000 ped., 19.X.1900, *Pringle* 9042; in valle Toluca, X.1827, *Berlandier* 1136; prope Xochicalo ad Cuernavaca, XII.1887, *Seler* 389; San Anton prope Cuernavaca, 14.X. 1904, *Seler* 4197; in valle Toluca, X.1827, *Berlandier* 1136; **Oaxaca**: Oaxaca, 20.XI. 1895, *Seler* 1358; prope Oaxaca, XI.1840, *Galeotti* 7137; in valle Oaxaca, 5000 ped., 30.X.1894, *L. C. Smith* 412; prope Oaxaca, 5100–5800 ped., 8.IX.1894, *Nelson* 1215; Sierra San Felipe, 6000 ped., 11.VI.1894, *Pringle* 5870; in Sierra San Felipe, 7.IX.1921, *Conzatti* 4212; in Sierra de la Soledad, 20.XI.1895, *Seler* 1358; La Bastolo Youhtepec, 7.I.1896, *Seler* 1658; **Puebla**: Caxcotlan, 7000–8000 ped., IX.1909, *Purpus* 4162; **Vera Cruz**: Orizaba, 1853, *Müller*; Borrego, Orizaba, 16.IX.1866, *Bourgeau* 3046; inter Vera Cruz et Orizaba, *Müller* 598; in collibus; aridis prope Orizaba, 29.IX.1923, *Smyth* 164; Orizaba, 4000 ped., 25–31.VII.1891, *Seaton* 144, 35.

2. *A. Mociniana* comb. nov.

Hyptis Mociniana Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr. 12:128.1848 per specim. in Mexico a Moçino et Sesse lectum constituta est; typum verisimiliter verum e herb. Lambertiano in herb. Kew. vidi.

H. spinulosa Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr. 12:128.1848 per specim. in Mexico a Moçino et Sesse lectum constituta est; typum olim in herb. Lambert. hodie in herb. horti bot. Oxon. vidi.

H. stellulata var. *Sinclairi* Benth. in DC. Prodr. 12:128.1848 per specim. in Mexico prope Acapulco a Sinclair lectum constituta est; typum in herb. Kew. vidi.

Mesosphaerum mocinianum Kuntze, Rev. Gen. 2:526.1891 (nomen).

H. alopecuroides Briq. in Ann. Conserv. Geneve 2:201.1898 per specim. in Costa Rica prope San Mateo a Biolley (in Pittier et Durand no. 7099) lectum constituta est; typum in herb. Delessert., isotypum in herb. Mus. Brux. et Smithson. vidi.

H. Biolleyi Briq. in Ann. Conserv. Geneve 2:200.1898 per specim. in Costa Rica inter San Mateo et S. Ramon a Biolley (in Pittier et Durand no. 7010) lectum constituta est; typum in herb. Delessert., isotypum in herb. Mus. Brux. vidi.

Mesosphaerum alopecuroides Briq., loc. cit. (nomen).

M. Biolleyi Briq., loc. cit. (nomen).

Suffrutex altitudine 1–3 m. ramulis gracilibus divaricato-ascendentibus obtuse quadratis sulcatis, pilis brevibus extensis sparse vestitis, internodiis 3–8 cm. longis; foliorum laminis sat tenuibus anguste ovatis, 3–8 cm. longis,

1.5–3.5 cm. latis, acutis vel leniter acuminatis, in basi saepius rotundato-truncatus vel rotundatis, margine subdupliciter serrulata, crenis ad 1 mm. altis, pagina superiore hirtella, inferiore villosula vix tomentosa pallidiore vix tamen incana, petiolis 3–12 mm. longis elatis; verticillastris in maturitate 8–12 mm. diametro, *maximam partem in spicas cylindratas densas confertis*; calycum florentium tubo 1.2–1.5 mm. longo, dentibus 2.5–3.5 mm. longis, saepius anguste marginatis et *ad margines* solummodo hirtellis, in maturitate tubo 1.5–2 mm. longo; corollarum tubo 2.8–3 mm. longo; nuculis circa 1 mm. longis.

MEXICO: **Guerrero**: prope Acapulco, *Palmer 128*; prope Acapulco, *Sinclair*; prope Acapulco, *Barclay*. **Vera Cruz**: sine loco, *Mocino et Sesse T*; in valle Cordoba, 14.I.1866, *Bourgeau 1707*; prope Zacuapan in Barranca de Santa Maria in agris, XII.1906, *Purpus 2285*; prope Atoyac, XII.1882, *Kerber 170*; prope La Purga, 27.I.1906, *Greenman 223*; Orizaba, *Botteri 647*; **Chiapas**: prope Teopisco, 30.XII.1906, *Collins et Doyle 121*; prope San Sebastian, 14.I.1907, *Collins et Doyle 189*.

GUATEMALA: prope Jumaytepeque, Santa Rosa, *Heyde et Lux 4109*; prope Gualan, 420 ped., *Deam 365, 366*; prope Agua Caliente, 10.II.1917, *Holway 848*;

HONDURAS: in silvis montanis ad Copan, 8.I.1897, *Seler 3330*; prope Ampola, Isla Tigre, 14.II.1922, *Standley 20714*.

SAN SALVADOR: in monte ignivomo San Salvador 9.I.1898, 7000 ped., *Niederlein 261*; sine loco, XII.1905, *Velasco 8872*; sine loco, *Calderon 2281*; prope Ahuachapan, 1923, *Padilla 509*; prope Ateos, 17.IV.1922, *Standley 23413*; inter San Martin et Laguna de Ilopango, 1.IV.1922, *Standley 22616*; prope San Vicente, 2–11.III.1922, *Standley 21222*; prope Ahuachapan 800–1000 m., 9–27.I.1922, *Standley 19945*; prope San Salvador, 650–850 m., 20.XII.1921–4.I.1922, *Standley 19153*.

NICARAGUA: prope La Paz ad vias, 31.I.1903, *Baker 210, 663*; Matagolpa, 500 m., 27.II.1894, *Rothshuh 507*; prope Grenada, XII.1869, *Levy 296*.

COSTA RICA: prope Nicoya, 1.1900, *Tonduz 13656*; prope San Mateo, *Pittier et Durand 7099*; prope San Mateo, 200 m., 20.I.1892, *Biolley 7103*; San Mateo et San Ramon, 400 m., 25.I.1892, *Biolley 7010*.

3. A. Seemanni comb. nov.

H. Seemanni Gray in Proc. Amer. Acad. 21:407.1886 per specim. in Mexico occ. in Cerro de Pinal a Seemann (n. 1500) lectum constituta est; typum in herb. Gray., isotypos in herb. Kew. et Mus. Brit. vidi.

H. Seemanni var. *stenophylla* B. L. Robins. in Proc. Boston Soc. Nat. Hist. 31:267.1904 per specim. in Mexico prov. Sonora prope Badehuache a Lloyd (no. 450) lectum constituta est; typum in herb. Gray. vidi.

Frutex habitus Buddleiae ramulis gracilibus subteretibus dense hispidulo-villosulis, internodiis 2–5 cm. longis; foliorum mediorum laminis oblongo-lanceolatis, maximam partem 5–8 cm. longis, 1–2 cm. latis, acutis, in basi rotundatis interdum angustatis, margine serrulata, crenis .5 mm. altis, pagina superiore hirsuta, inferiore villosa pallidiore interdum subglabra, petiolis 5–10 mm. longis elatis; floribus in paniculis *gracilibus moniliformis* subnudis, glomerulis compactis subglobosis incanis inter se 10 . . . 8 . . . 5 . . . 3 mm. distanti-

bus, *maturis* 5–7 mm. diametro; calycibus florentibus 1.5 mm. longis extus villosis, ore valde hirsuto, dentibus circa .4 mm. longis, in maturitate tubo paulo aucto; corollarum tubo 2 mm. longo; nuculis 1 mm. longis.

MEXICO: Rio de Aros, 7000 ped., *Townsend et Barber* 400; **Chihuahua**: in quercetis inter Reforma et Agua Caliente de Huachara, 25.XII.1904, *Endlich* 750; Batopilas, 5500–6500 ped., 4–5.X.1898, *Goldman* 198; sine loco, *Palmer* 177; Cerro de Pinal, XII.1848, *Seemann* 1500 T; **Sonora**: Badehuache, 2.XII.1890, *Lloyd* 450; prope Alamos, 1890, *Palmer* 398; **Sinaloa**: Batel, *Dehesa* 1624; Villa Union, I.1922, *Ortega* 4441; Balboa, I. 1923, *Ortega* 5050;

Index Nominum.

Asterohyptis Mociniana Epl.

Asterohyptis Seemanni Epl.

Asterohyptis stellulata Epl.

Hyptis alopecuroides Briq.

Hyptis Biolleyi Briq.

Hyptis mociniana Benth.

Hyptis pubescens Benth.

Hyptis Seemanni Gray

Hyptis Seemanni var. *stenophylla* Robins.

Hyptis spinulosa Benth.

Hyptis stellulata Benth.

Hyptis stellulata var. *Sinclairi* Benth.

Mesosphaerum alopecuroides Briq.

Mesosphaerum Biolleyi Briq.

Mesosphaerum mocinianum Kuntze

Mesosphaerum pubescens Kuntze

Mesosphaerum stellulatum Kuntze.

Reproduction in the rusts

MABEL A. RICE

(WITH PLATES 4-6)

We have apparently reached a period of rapid advance in our knowledge of sexual reproduction in the rusts. The results gained from cultural methods, applied so successfully by Craigie (1927) under the leadership of Buller have quite re-established the tentative views of Meyen, Tulasne, and de Bary as to the nature and functions of spermogonia and spermatia though Craigie, Buller, R. Allen and Andrus make no reference to this earlier work.

Meyen (1841) writes: "Eine genauere Untersuchung dieser eigenthümlichen Bildung, welche den Aecidien-Pusteln stets vorangeht, so wie die Berücksichtigung der räumlichen und zeitlichen Verhältnisse, unter welchen jene beiden Bildungen zu einander stehen, veranlassen mich zu der Meinung, dass wir hier verschiedene Geschlechter eines und desselben Pilzes vor uns haben, dass nämlich das *Aecidiolum exanthematum* des Herrn Unger die männliche oder befruchtende Bildung der darauf folgenden wahren, sporen-artige Bläschen enthaltenden *Aecidium-Pustel* ist."

Tulasne (1854) states his agreement with de Bary, saying that "le premier (*l'Aecidiolum*) lui a semblé, comme à nous, offrir tant d'analogie avec les spermogonies des Lichens, qu'il ne fait pas difficulté de lui accorder le nom de ces organes et la même valeur physiologique, quelle qu'elle soit d'ailleurs. Cette valeur est effectivement incertaine, et le sera sans doute longtemps encore."

De Bary (1887) writes:

"The spermogonia, where they occur, are always the precursors of the aecidia which belong to them, that is they are always present in a fully developed state when the first beginnings of the aecidia make their appearance in their neighborhood. All these facts point to a physiological relation of the two organs to one another similar to that which exists between the spermogonia and sporocarps of the *Collemaeae*. But a more certain proof of this relation is still wanting; the organs in question must therefore for the present be classed with those in which the physiological import is doubtful."

Brefeld (1888) on the other hand disclaimed any sexual nature for the higher fungi and considered the spermatia of conidial nature. He writes: "Die Spermatien der Ascomyceten und namentlich der flechtenbildenden Formen unter diesen sind nur Conidien, . . ."

"Die Spermatien (of the Uredineae) in den kleinen Fruchtanlagen der Spermogonien sind die einfachen Conidien."

Arthur (1905), as a part of his new terminology for rust sori, substitutes pycnium for spermogonium and pycniospores for spermatia. In a later discussion of this terminology Arthur and Kern (1926) state: "It is proposed to use the term *pycnium* for the sori with inefficient spores. Neither the term nor the manner of defining it raises the question whether or not these are vestigial sex organs." Discussing the subject of sexuality among the rusts, Arthur (1929) supports this use of the term *pycnium*, writing: "Nevertheless, no process of sexuality embodying such a high type as just indicated (male and female organs) has yet been found in any species of the rusts although pycnia have from first to last maintained their reputation as male organs and correspond to such in details of gross and minute structure and in time and place of their appearance." He writes further, with reference to Craigie: "they (the pycniospores) may exert a quickening influence upon the development of the aecia."

Cunningham, (1932) however, discards the term *spermogonium* because of its sexual connotation. He states: "As this structure is not a male organ it cannot be termed a spermogonium." Like Arthur he objects to the term *pycnidium* on the ground that the rust structure is not homologous with the pycnidium of Ascomycetes. He modifies Arthur's term pycnium to pycnisorus but he adopts Arthur's term *pycniospore*.

Craigie (1927), following Arthur except for one difference in spelling, calls the receptacle a pycnium and the spores pycnosporos which deBary called respectively spermogonium and spermatia. Craigie seems, however, to have made this choice because of the relation of these terms to pycnidium and pycnidiospores, terms commonly used for conidia borne in a flask-shaped receptacle, and seems to be following Brefeld and to be denying that these rust spores have any sexual character, at the same time that he is announcing the demonstration of their differentiation as plus and minus and their function in sexual reproduction. He writes: "The pycnosporos are not functionless male gametes but are simply conidia corresponding to the uninucleate oidia which appear on the monosporous mycelia of such heterothallic Hymenomycetes as *Coprinus lagopus*, *Coprinus niveus*, *Stropharia semiglobata*, and *Collybia velutipes*." This might seem to imply the assumption of such sexually differentiated races as Dodge (1924) has found in *Caeoma nitens*, but in the absence of any statement from Craigie as to how such conidia germinate and the specific part they play in developing the aecidium the statement is rather confusing.

The historical survey of views concerning the function of the spermatia of the rusts made by Blackman and by Klebahn in 1904 and by

Moreau in 1913 continued to be adequate for the subject until the work of Craigie was published in 1927. They held respectively that the "spermatia are male cells which have now become functionless"; that "die Spermogonien als Organe anzusehen, denen gegenwärtig im Leben der Rostpilze keine Bedeutung mehr zukommt, . . . Man könnte auf den Gedanken kommen, dass die Ausscheidung eines Teils seiner Substanz für die Weiterentwicklung des Pilzes nützlich wäre"; "que nous nous trouvons en présence de deux opinions presque également soutenables: ou bien ce sont des spores asexuelles et alors elles ne jouent pratiquement aucun rôle, ou bien ce sont des vestiges de gamètes mâles et jusqu'ici aucune tentative pour retrouver les vestiges des gamètes femelles correspondants n'a donné pleine satisfaction. C'est la découverte d'organes sexuels femelles vestigiels qui seule, dans l'état actuel de nos connaissances, nous paraît capable de forcer l'opinion en faveur de la nature sexuelle des spermaties."

It becomes now more than a theoretical question to choose between the two terms, spermatia and pycniospores. In support of the former term excellent evidence for the morphological identity of spermatia and microconidia, which Tulasne (1861, 1931) distinguished by the criterion of non-germination or germination respectively, may be found, in the three groups Ascomycetes, ascomycetous lichens, and rusts, by a review of the different types which are present in each of these groups.

In the Ascomycetes the *Sclerotinias* of Woronin (1888) bud off what he called "spermatienähnlichen Sporidien" from all parts of the mycelium and from conidia and ascospores. *Sclerotinia Duriaeanae* (Whetzel, 1929) produces microconidial sporodochia. Whetzel did not attempt the germination of the microconidia but states; "They more probably function as do the spermatia of the rusts (Craigie 1927)." *Neurospora sitophila* (Dodge, 1930) bears, on branches of the mycelia, microconidia which Dodge calls "clearly homologous with the microconidia of *Sclerotinia*"; *Sclerotinia Gladioli* (Drayton, 1932) bears microconidia in sporodochium-like masses; *Pleurage anserina* (Ames, 1932) bears microconidia on branches of the mycelium. Drayton (1932), Dodge (1932), and Ames (1932) have proved these microconidia to be functional male gametes.

An intermediate between this diffuse type of bearing male cells and the spermogonium and spermatia of the *Collema* and *Physma* studied by Stahl (1877) is illustrated in the form of *Collema pulposum* studied by Bachmann (1912). In this last case the reduction in number and mobility of the spermatia is correlated with the great length of the trichogyne which thus "seeks out" the spermatia. This sessile habit of the spermatia leads over to the single and sessile antheridia of *Ascobolus magnificus* and *Py-*

ronema, and to the still more reduced habit of *Sphaerotheca*, *Ascobolus furfuraceus*, *Gymnoascus*, etc.

The occurrence of spermatia in crusts on stromata is a different type. The occurrence of spermatia in such crusts under and following conidial crusts is figured by Higgins (1914) for *Coccomyces hiemalis* and is reported by Backus (1932) for the same fungus. In the rusts one finds such a caeomatous habit of bearing spermatia in *Peridermium cerebrum* and *Peridermium Strobi* (Arthur's (1929) subcortical type).

There is also found in each of the three groups: Ascomycetes, ascomycetous lichens, and rusts, the very different type of spermatial development in pycnidium-like receptacles. In the Ascomycetes pycnidium and spermogonium are linked by forms in which spermatia develop after the pycniospores in the base of the same pycnidium. This is figured by Longyear (1904) for *Guignardia Bidwellii*, by Stewart (1916) for *Guignardia aesculi*, by Klebahn (1918) for *Mycosphaerella maculiformis*, and by Higgins (1920) for *Sphaerella Bolleana*.

For spermatia borne in separate spermogonia, in the Ascomycetes Higgins (1914) figures *Mycosphaerella personata*; in the lichens Stahl (1877) figures the characteristic type for *Physma compactum*. This is in general the type so common among the rusts although there are characteristic differences. The well developed wall of the lichen spermogonium is lacking in the rusts and the paraphyses of the rust spermogonium are lacking in the lichens. With the subepidermal type of Arthur's classification as the normal, the flask shape of the rust spermogonium varies from the high, stalked spermogonium of *Caeoma nitens* to the other extreme of Arthur's subcuticular type where the flask shape is much flattened and paraphyses are few or lacking. In the greater development of paraphyses and in the abundance of a sweet sticky secretion the spermogonia of the rusts seem the more highly developed organs, adapted to terrestrial conditions and insect dissemination. Rathay (1883) established by observations upon twenty different rusts the facts that insects are attracted by a reduction sugar present in the fragrant exudate of the spermogonia and that spermatia are carried in the exudate. He made records of the species and the relative numbers of insect visitors and concluded "dass die Insecten zu den reifen Spermogonien der Rostpilze in einer sehr vollkommenen Weise gelockt werden."

In considering the sexual nature of spermatia and microconidia such confusion as Craigie's might be avoided by following Allen (1929) in recognizing the distinction between (1) characters which distinguish gametes, sex organs, or individuals as male or female and (2) characters which regulate syngamy. The latter are to be regarded as the primitive factors in sex-

ual reproduction since they include the capacities arising with sexual maturity. Cells fuse because they are mature, and have gained different powers with that maturity. Spermatia are produced because the mycelium which bears them is mature and they fuse with other cells because, as cells, they are sexually mature. That they differ structurally and functionally from egg cells is an adaptation to facilitate this fusion. As a familiar illustration,—cells of *Spirogyra* filaments develop in a more or less dense mass where they might readily fuse at any time but they continue their development by division only, until maturity. Maturity brings a change from the asexual habit to the habit or capacity for cell fusions. At sexual maturity conjugations may occur between cells in the same or in different *Spirogyra* filaments. From such fusions it is postulated that organisms may result which are better equipped for their environment and have a better chance for survival. The initiation of variation and its degree may be increased by cross-fusions (mixie). Possibly this advantage determines the perpetuation of the fusion of unlikes. At least it is obvious that many devices regulate syngamy in the interests of the less certain cross-fusions. Allen illustrates by dichogamy and heterostyly in the seed plants upon which may depend the possibilities of self-, close-, or cross-pollination and subsequent syngamy. He also places in this category the various compatibilities which result in group intra-sterility and inter-fertility in such a species as *Nicotiana*. By holding to these distinctions, as Allen points out, the difficulties of thinking in terms of sex of several plus and minus races disappear. When *Schizophyllum commune* (Kniep, 1922), *Hypholoma fasciculare* (Funke, 1924), and *Coprinus lagopus* (Hanna, 1925) are reported to be four-sexed we should think, not of bipolar characters of maleness and femaleness, but of multipolar characters which, through group compatibility or incompatibility, further or inhibit syngamy. This distinction obviates Craigie's objection to the term spermatia for spores which show plus and minus characters. The property of maleness, a character of sexual differentiation, placed by Allen in his first category may coexist with degrees of compatibility, characters favoring or hindering syngamy, placed by Allen in his second category. Ruth Allen (1930) fails to draw this distinction when she writes of the spermatium: "Nor can it be considered a vestigial male organ, for, as Craigie has pointed out, half of the pycnia are of one sex and half of the other, although they look alike." In a later paper Ruth Allen (1932) writes: "The word 'spermogonium' implies a male structure. It should not be forgotten, however, that when nectar is interchanged between two infections of different sexes each fertilizes the other." Here evidently the term "male structure" refers to a first category character; likewise the term "fertilization," but the phrase,

"two infections of different sexes" refers, as she has explained earlier, to the plus and minus character of two monosporidial mycelia. These are, I think, characters of the second category.

We shall do well to use terms with the utmost care in a field so complicated as that of sexual reproduction in the fungi and algae. The distinctions which I have attempted by the use of Allen's categories raise other questions of terminology. Compatibility and incompatibility imply that mature germ cells which are functionally effective in a given combination may be quite non-functional in another. They do not imply the sex of Allen's first category. The genetic origin of these evolved differences in compatibility is more easily explained when they fall into two groups only and are, as Gwynne-Vaughan (1932) suggests, "complementary" but there are multipolar groups to be reckoned with and in these the compatibility relations will probably give the key to the solution. In the fungi perhaps the best known cases of multipolarity in compatibilities are among the Hymenomycetes where their origin in the basidium indicates a segregation of factors by reduction division.

Allen (1932) in a more recent discussion of the sex problem attempts to name and classify the genetic factors which have to do with sex as contrasted with the sex characters themselves. He recognizes three genetic classes. He describes maleness and femaleness as the effects of (1) *sex-potency factors* which are present as a pair of potentials in every organism. The exceptions to the resultant hermaphroditism he sees as the inhibiting effect of (2) *sex-tendency factors* located possibly in the X-Y chromosomes. The many other diverse genetic factors which influence sex expression, Allen groups under the term (3) *sex-influencing factors*. Allen's second discussion, by the illustrations of the workings of sex-potencies and sex-tendencies, clarifies our conceptions of heterothallism even though it is from the Angiosperms that he draws his most distinctive illustration. The heterothallism brought about by the inhibition of a sex-tendency factor upon the sex-potency factors which effect a homothallic condition is a structural heterothallism, a first category sex character. It becomes clear, by contrast, that the heterothallism under discussion in the fungi is one of incompatibility.)

(Allen notes the infrequency of the occurrence of structural heterothallism among the Angiosperms. His illustrations from the sporophytic stage of the Angiosperms would, according to Blakeslee (1906), be examples of heterophytism rather than heterothallism. Allen makes the distinction in pointing out that the gametophytic stage of the Angiosperms is always functionally unisexual. Too little is known yet about the Thallophytes in relation to sex classes to generalize but it is possibly significant that several

recent reports announce determinations of self sterility in connection with homothallism. Rosenvinge (1929) has reversed Darbishire's (1899) statement that *Phyllophora Brodiaei* is dioecious. He finds both sex organs present on each plant although they do not function. Drayton (1932) writes of *Sclerotinia Gladioli*, "It was also demonstrated that the receptive bodies of each isolate do not react with their own microconidia; that is, they are all self-sterile." Ames (1932) reports *Pleurage anserina* to be hermaphroditic but self-sterile. Gwynne-Vaughan (1932) reports two strains of *Ascobolus magnificus* in which all thalli are capable of bearing both male and female organs but in which fruit can only be formed when two "complementary" mycelia are intermingled.

Gwynne-Vaughan does not admit this difference in complement in the strains of *Ascobolus magnificus* as a distinction of sex. Although she does not give a name to the character, her illustration of self sterility in *Primula* suggests incompatibility. She sees the character in *Ascobolus magnificus* operating through the male and female organs, and, in such fungi as lack the male or female organs or both, she sees it acting as a substitute character which gives physiologically the same effects as sexual union. It seems to me that Allen's system of two sex categories, as outlined above, is preferable as a system by which to distinguish the quite different characters which we are coming to realize are confused under the convenient terminology introduced by Blakeslee (1906).

In his work with *Neurospora* Dodge (1932) has called those races heterothallic that will produce perithecia only when two different strains are brought together. Dodge reports that this mating of strains may be between mycelia obtained either from ascospores, from macroconidia, or from microconidia which he has germinated in often-repeated experiments. Each mycelium, however, Dodge points out produces microspores or macrospores in addition to ascogonial coils and the primordia of perithecia. He finds that either macroconidia or microconidia may function in initiating perithecial development. Upon the basis of these data Dodge, one would think, by his reference to the Kniep-Correns theory, draws the same distinctions that Allen has made for the Angiosperms with reference to sex-potency and sex-tendency factors. He writes, "Kniep points out that one could assume with Correns in accounting for the reactions of our so-called heterothallic Ascomycetes that each haploid mycelium contains potentialities of both male and female sexes, but that there are genes, determinators, that impress on such a mycelium either a male or a female stamp when it comes to the origin of fruit bodies." Dodge states that any monosporous mycelium of *Neurospora* "is, to all intents and purposes, unisexual when it comes to sexual reproduction." This must be, however,

because of self-sterility rather than the segregation of sexes. Turning to *Pyronema* where both of the sex organs are known, he sums up: "The development of antheridial branches as distinct from oogonial branches in *Pyronema* is a case of sex differentiation and not sex segregation. It is a coming to maturity of the mycelium."

It seems clear that Craigie is wrong in likening the "pyncospores" to the ^{con}sporidia of the Hymenomycetes. It is today a generally accepted fact that the teleutospore with reduction division in the promycelium is homologous with the basidium of the Hymenomycetes. The homology may be extended to include the Ascomycetes. Harper (1905) writes: "If the evidence advanced by Mottier and Williams that a reduction division occurs in the development of the tetrasporange be confirmed, it is plain that the homologue of the ascus and the teleutospore, and of the basidium as well, is in the tetrasporange and not in the carpospore, as many have been inclined to assume." The spermatia, Craigie's "pyncospores," are haploid spores, developed upon a mycelium, the outgrowth of a haploid sporidium. It is not strange then, that with such a derivation there should be compatibility or incompatibility in the reactions of the gametophytic mycelia. This heterothallism belongs in Allen's second category: it is a functional rather than a morphological dioecism.

The discovery that there are degrees of compatibility in the rusts is a distinct contribution but this discovery merely brings the rusts into line with the other great groups of plants in which an increasing mass of evidence leads us now to expect to find that syngamy is regulated in the interests of cross-fusion. The crux of Craigie's work is his evidence that the spermatia, which have long been thought functionless, are in reality a necessary link in the production of aecidiospores. Craigie seems only concerned with heterothallism when he lists "three ways in which pustules of monosporidial origin may change from the haploid to the diploid condition" and he confines himself to the mention of fusions between plus and minus mycelia or plus and minus "pyncospores." Ruth Allen recognizes the two distinct problems. Yet curiously enough her reports of attempts to find out by cytological methods, the details of fertilization she entitles merely, "Heterothallism in *Puccinia graminis*" (1930), and, "A cytological study of heterothallism in *Puccinia triticina*" (1932). .

REVIEW OF LITERATURE

Comparatively little cytological work upon reproduction in the rusts has been published since Craigie's discovery. Hanna (1929) found that aecidia of *Puccinia graminis* in monosporidial infections were composed of a haploid mycelium and were sterile, while infections in which spermo-

gonial nectar had been 'mixed produced aecidiospores from a diploid mycelium.

Andrus (1931) found evidence of heterothallism in *Uromyces appendiculatus* and *Uromyces Vignae* and also made a cytological examination of the spermogonial and aecidial development of these rusts. He emphasizes the latter by his title: Sex in *Uromyces appendiculatus* and *Uromyces Vignae*. Andrus regards the spermatia as functional male gametes. He interprets as trichogynes the hyphae which he finds projecting through stomata or between epidermal cells. In a few of these he observes a binucleate condition. He has not been able to trace this "trichogenous hypha" to the egg cell which he locates at the base of each spore chain in the aecidium but he interprets the "two-legged" cells which he finds there as egg cells each with a trichogenous branch and a foot-cell. He figures the passage of what he believes the nucleus of the spermatium from this trichogenous branch up into the egg-cell. These "ruptured hyphae" and their binucleate condition may, I think, be open to another interpretation since the bean rust is an autoecious rust. It is a question as to whether the hyphae which Andrus saw at the surface of the leaves are not infection hyphae from aecidiospores. An intermingling gametophytic and sporophytic mycelium has frequently been reported for rusts of this class. Sappin-Trouffy (1896) mentions such a condition for *Puccinia Violae*; Fromme (1914) for both *Puccinia Violae* and *Puccinia Claytoniata*. Olive (1908) reports intermingling mycelia for *Puccinia Podophylli*.

Ruth Allen (1930, 1932) has published two papers which give cytological details of stages in the reproduction of *Puccinia graminis* and *Puccinia triticina*. Her data upon the two critical points in the reproduction process (the function of spermatia, and the initiation of the spore chains in the aecidium) effect an alteration in her theories as given in the first and the second papers. Binucleate cells found in the region of spermogonia in the mycelium of *Puccinia graminis* lead her to place the initiation of the sporophytic generation there but she emphasizes the view of Cragie that the spores which function there, either directly or indirectly, are non-male, plus and minus pycniospores. In the mycelium of *Puccinia triticina*, however, she finds hyphae which penetrate the stomata of the host from below and end at once in enlarged finger-like tips. In the substomatal spaces she finds binucleate and multinucleate cells. Allen does not report seeing fertilization but the nuclear conditions described in the substomatal hyphae, taken in conjunction with Cragie's evidence that spermatia play a part in the development of aecidiospores, she regards as indirect evidence that these protruding hyphae are "receptive hyphae." She returns, therefore, to the idea of the earlier mycologists that spermatia are functioning

male gametes, instead of pycniospores. Allen does not refer to the fact that similar protruding hyphae were earlier reported, although lacking evidence of fertilization they were not regarded as trichogynes. I am not sure whether de Bary (1887) was the first to observe them, but his description fits Allen's figures. "In young groups of aecidia a phenomenon is observed not infrequently and without great difficulty, which seems to be in favor of the supposition that there is an archicarp duly equipped for conception; short obtuse hyphal branches project from some of the stomata like the tips of the trichogyne in *Polystigma* and may be traced here and there to a young perithecium." Klebahn (1904) has also described the same structures. "Man findet vielfach Hyphenknäuel, die sich unter den Spaltöffnungen angesiedelt haben, und durch den Spalt selbst ein kleines Hyphenbündel nach aussen schicken; am äusseren Rande des Spaltes endigen die Hyphen gewöhnlich mit einer kleinen Anschwellung. Gar nicht selten werden auch Spermatien bemerkt, welche an diesen Hyphen zu sitzen scheinen. Dies ist aber nichts auffälliges, denn die Spermatien finden sich in Menge auf der Epidermis und dürften sich also besonders leicht im Schutz der Erhöhungen und Vertiefungen der Spaltöffnungsansammeln."

In discussing the second critical point (the initiation of the spore chains in the aecidium) Ruth Allen emphasizes again the significance of the multinucleate cell. In *Puccinia graminis* she finds this first in the anlage of the aecidium and interprets it as the result of nuclear division in the sporophytic mycelium. In *Puccinia triticina* she finds the multinucleate condition also in hyphae of the sub-stomatal chamber and she interprets this as due to the entrance of many spermatial nuclei into one "receptive hypha." It is true that a "receptive hypha" functioning as a trichogyne may receive several male nuclei. Wolfe (1904) figures this for *Nemalion*. The hypha may merely transmit these spermatial nuclei to distant egg cells but here again we have precedent for considering the trichogyne as the accessory of a single egg cell while Allen seems to think that these same nuclei (the many male nuclei and the "native nucleus" of a hyphal cell) are present in the multinucleate cells of the aecidium from which she reports that the spore chains bud off. The actual contacts of spermatia with the trichogyne were not seen and the supposition that the multinucleate condition is the result of nuclear divisions, as Allen first suggested, would seem to be at least as likely, as that of the entrance of many spermatia. This supposition that the nuclei of many spermatia are present in the multinucleate cell of the aecidium makes more difficult any explanation for the condition reported by Allen (1930) for *Puccinia coronata* where she reports the finding of multinucleate cells, often of monstrous size, "in practically 100% of all the older sterile aecia."

Multinucleate cells in the base of an aecidial primordium have been frequently reported. Allen, in her paper upon *Puccinia graminis* lists nine workers since and including Blackman who report the phenomenon. The majority of these report cases of tri- and quadri-nucleate cells which give rise to chains of spores of the same nuclear number. Fromme (1912) in addition to this figures one case for *Melampsora lini* of a spore-mother cell with eleven nuclei. He interprets all the cases as due to the fusion of more than two cells for the formation of the "basal cells." Colley (1918) reports multiple fusions in aecidia of *Cronartium ribicola* and finds the number of polynucleate spores relatively so small that he concludes "either the extra nuclei so common in the basal cells degenerate or the complex basal cell gives off more than one binucleate spore chain." He finds some evidence in *Cronartium ribicola* that aecidiospore chains arise by branching from a large basal cell as Dittschlag (1910) and Hoffman (1912) figure for *Puccinia falcariae* and *Endophyllum Sempervivi*, respectively, Olive (1908) alone reports multinucleate cells in the aecidium as a possible normal condition for rusts in general. "That multinucleated cells are formed probably as regular occurrences during the earlier stages in the development of the young aecidia is indicated by their discovery during the course of this investigation in at least eight or ten species of rusts. I am therefore convinced that they are perfectly normal occurrences, and that they result simply from the nuclear divisions going on much faster and thus getting ahead of cell divisions." It is to be noted that Olive places the occurrence of the multinucleate cells after the cell fusions at the base of the spore chains. "While the part which these multinucleated cells take in the development of the aecidium is as yet somewhat obscure, the evidence appears to point to the conclusion that they are sporophytic structures and that they result from the stimulated growth which follows the sexual cell fusions."

Allen finds no cell fusion of the characteristic Christman type. In the earlier paper she treats the many cases heretofore reported of this type of fusion as possible instances of homothallism in the rusts. In her later paper she is inclined to question the occurrence of such fusions as the initiation of spore chains. "It is evident that the presence of a 2-legged basal cell is not in itself proof of fusion. In the past the presence of a few 2-legged cells in the layer of basal cells has sometimes been the only evidence offered that the sporophyte originated by fusion of pairs of uninucleate cells in the sporogenous area in the aecium. Without a study of younger stages, there is a risk of error in this assumption."

Fusions as the initiation of basal cells are the only type which are discussed by Allen. It seems to me that fusions might be considered in con-

nection with the development of the multinucleate cells in the aecidium. Allen does not report seeing any such fusions but the irregular lobes figured in her Plate 11, A-G suggest the possibility. This is one of the considerations which "the background of a red alga ancestry" (Dodge 1929) would suggest and Allen (1932) now considers the "probability of phylogenetic relationship between the two groups."

INVESTIGATIONS

Materials and methods

I have made a cytological study of spermogonial and aecidial stages of *Puccinia Sorghi* and also, to a lesser degree, of *Aecidium punctatum*, *Puccinia Violae*, and *Uromyces Caladii*. The three latter were all studied from field collections of the infected hosts: *Hepatica acutiloba*, *Viola cucullata*, and *Arisaema triphyllum*, respectively. For the study of *Puccinia Sorghi* teleutospores were supplied by E. B. Mains; *Oxalis* plants were collected from greenhouses at the New York Botanical Garden, Columbia University, and Wheaton College as it was too early for *Oxalis* in the field when the work was started. These plants were of two species: the familiar garden weed, *Xanthoxalis stricta* (L.) Small, and a small red-leaved form abundant as a weed in the plant house at Columbia University which, according to Bailey, is the tropical *Oxalis repens*, Thumb. a variety of *Oxalis corniculata*, Linn. (*O. stricta* L.), *Xanthoxalis corniculata* (L.) Small. Both varieties proved susceptible to the rust but the larger leaves of *Xanthoxalis stricta* were used for the cytological work. Inoculations were made both by moistening leaves with water into which teleutospores had been scraped, and by suspending the rusted corn leaves above the *Oxalis* plants by pressing the leaves into dishes of mud and inverting these over glass cylinders, after the method described by Allen. Both methods gave abundant infections. Monosporidial inoculations were not made.

Samples of leaves from inoculated plants were fixed at two-day intervals from two days after inoculation until after the discharge of aecidiospores. In the delicate leaves of *Oxalis* Flemming's medium solution caused shrinking of the hyphae. Fixations were made in Flemming's weak solution, Allen's B-15, Carnoy and 50% alcohol. Flemming's weak solution and Allen's B-15 proved the most satisfactory fixatives. For the fixation of *Puccinia Violae*, *Uromyces Caladii*, and *Aecidium punctatum* Flemming's medium solution was used. Sections were cut 5 μ or 7.5 μ thick and were stained with the triple stain.

OBSERVATIONS

Puccinia Sorghi. The first visible signs of infection on the *Oxalis* are yellow flecks which appear in from five to seven days after inoculation. They develop on the blades of the leaves but not on the petioles. From the inoculations described above the infections were merely sporadic. It was therefore difficult to detect the earliest signs of infection among the many healthy leaves. Spermogonia appeared in eight or nine days as tiny orange pimples in close clusters on both surfaces of the leaves. They are, however, more abundant on the upper leaf surface. They exude nectar abundantly for several days. Aecidia develop outside the clusters of spermogonia, forming, in the case of isolated spermogonial clusters, a complete circle around the cluster. They are erumpent in about two weeks after inoculation. The peridium is shaped like a slender jar with a slightly constricted mouth and is about three times the thickness of the leaf in height. The infected area is yellowed and is hypertrophied to twice the normal thickness of the leaf, chiefly by the elongation of the palisade parenchyma. The infected leaves age rapidly. By the time the aecidia of an infected leaf were all erumpent the leaf was generally withered and the plant with its indeterminate growth appeared quite healthy.

Aecidium punctatum. The stages of *Aecidium punctatum* were obtained from a single *Hepatica* plant which has been under observation for several years in a wood garden at Wheaton College. During this time rust has developed regularly on this one plant while none of the other *Hepaticas* in the garden plot have shown any rust. The rusted plant is sterile; the first leaves appear while the other plants are sending up blossoms. The folded leaves, when they first appear above ground, are punctate with spermogonia. Instead of growing in close-set clusters as do those of *Puccinia Sorghi*, single spermogonia dot thickly both surfaces of the leaves over all but the basal part of the blade. The brown hemispherical pustules glisten with an exudate when ripe and later persist as dry brown pimples. Aecidia develop within the same areas but open more frequently on the lower surface. The white peridium torn into four or more irregular lobes around the brown spores gives, at close view, a flower-like appearance to the aecidium. A second contrast to *Puccinia Sorghi* may be noted in the leaves of the *Hepatica* host. Instead of the localized changes described for *Oxalis* there is hypoplasia of the blade and hypertrophy of the petiole. The leaf is not yellowed but the blade is less divided than normal and stands erect on an abnormally long petiole as has been well figured by Arthur (1929). The rusted leaves do not live over winter after the habit of healthy *Hepatica* leaves. After four or five rusted leaves have appeared these are

followed by a whorl of healthy leaves. In June the green rusted leaves with their dried pustules stand erect in the center of a spreading circle of healthy leaves. In the fall there is no trace of the rusted leaves and sections of the persisting leaves do not show a mycelium.

Uromyces Caladii. Rust develops on *Arisaema triphyllum* with the unfolding shoot. The pale yellow spermogonia dot the surface of stem, petiole, leaf blades, spathe, and spadix. Accidia are most abundant on the leaf tissues. The gray-white accidia are much shallower cups than either *Puccinia Sorghi* or *Aecidium punctatum*. The material used for examination was erumpent with both spermogonia and accidia.

Puccinia Violae. No succession of stages was examined in the violet rust. The violet plants were found heavily infected at the time of their blooming. Both spermogonia and accidia were erumpent on thickened galls which were abundant on petioles and veins of the leaves.

Under microscopic examination I found in the rusted violet tissue binucleate hyphae which seemed somewhat like those described by Andrus for the bean rust as trichogynous hyphae (figs. 16, 17) but in reality, in my opinion, these hyphae extend through the stoma and are infecting hyphae from aecidiospores. Since the violet leaves at the time of fixation showed an abundance of ripe accidia there must have been full opportunity for a reinfection by aecidiospores. Binucleate hyphae could be traced from stomatal regions into the web of hyphae which separates the very loosely built parenchyma from the lower epidermis. This is the region where accidia develop. There may be some connection here but I have already called attention to the fact that the occurrence of binucleate hyphae intermingled with the uninucleate stage of the violet rust has been reported by Sappin-Trouffy (1896) and Fromme (1914) who consider that they are sporophytic hyphae developing from germinating aecidiospores. I have already called attention to the question of interpretation which this fact raises for the autoecious bean rust. It is true there may be other hyphae in these tissues which are protruded from stomata or between epidermal cells instead of being in process of entering as infection hyphae. I found in the violet leaf an occasional stoma plugged by a fragment of a dead, red-staining hypha much like those which I have found in *Oxalis*. (fig. 18). Earlier stages would, however, be needed before one could with certainty distinguish two types of stomatal hyphae in the violet rust.

I examined only a small amount of the rusted *Arisaema* tissue but here also red-staining hyphal plugs were frequently found in the stomata (fig. 20). Here also the autoecious character of *Uromyces Caladii* makes the interpretation of any binucleate condition indeterminate.

IN *Puccinia Sorghi* I have not yet found the stages showing infection of the *Oxalis* leaf by the sporidia of the rust but the infection hyphae in epidermal cells of the *Oxalis* leaf are abundant and conspicuous. Figure 1 shows one which was still alive in a leaf which was dotted with spermogonia and young aecidia fifteen days after inoculation. The original hypha is usually heavily sheathed and can be recognized long after the cell content is gone. In addition to sending branches into the intercellular spaces below they usually make a vigorous growth in the epidermal cell in the vicinity of the host nucleus. Such a tangled mass as is shown in the figure would presumably send out many hyphal branches. The cell figured lies close to a spermogonium on the left and the hyphae in the intercellular space on the left form part of the spermogonial tissue. By their perforation of an epidermal cell wall instead of entrance through a stoma, by their heavy sheath and persistent penetration beak they are readily distinguished from certain finger-shaped hyphae which I have found protruding from stomata of the *Oxalis* leaf.

Branches from the infection hyphae penetrate between the palisade cells and also form horizontal runners between the epidermis and the palisade. Long runners also follow the veins while the very slightly developed spongy parenchyma is crowded with a network of hyphae.

Haustoria are sent abundantly into the host cells from the intercellular hyphae. They are branched, much coiled structures arising from a short, slender entrance stalk. They have frequently more than one nucleus. They are in the great majority of cases coiled around the host cell nucleus. Invagination of the host cytoplasm is evident. Encasement or sheathing of the haustorium is rare but I have made no attempt to trace developmental stages of the haustorium in *Oxalis*.

From hyphal runners under the epidermis, particularly under the upper epidermis, short hyphae push out through the stomata. Sometimes as many as eight project through a single stoma. This can be seen best in a tangential section of a stoma but in a cross section view of a stoma the single hypha often proves, by a study of successive sections, to be one of a group. In figure 12, e, a fourth hypha is visible at an upper plane. These may usually be traced to separate origins from a runner or from several runners which crowd against the epidermis; less frequently they arise as a tuft from one branch. The cross section of the runner at the base of a hypha is a distinctive character in views of a single detached hypha. On account of the abrupt change of direction which these hyphae make in passing through the stomata this detached stomatal plug is the view most frequently seen of the branches. The central hypha in figure 4 shows the cell from the runner; also figure 18 from violet rust. The selection of views

on the plates is misleading in that this most characteristic view has been passed over and the occasional cases chosen which show more of the mycelium. These hyphae project from both the upper and the under surfaces of the leaf in the vicinity of spermogonia and aecidia. I have seen them just outside the paraphyses in surface views of epidermis which I have stripped from a leaf and mounted in lactophenol. Sections of the leaf prove that they are an almost constant accompaniment of the spermogonium. They are crowded so close to it that they seem to come from the ostiole but they are in reality outside the paraphyses. Figure 13 is taken from an outer vertical section of a spermogonium and shows the striking contrast between these short, blunt, red-stained tips and the long slender, pointed paraphyses. Figure 2 shows a stoma which lay just to one side of a spermogonium. The attachment of the projecting hyphae can be traced to the pseudoparenchyma of the spermogonium. Should these hyphae prove to be trichogynes there might prove to be significance in Fromme's finding spermogonia borne in the center of aecidia in *Puccinia Claytonia*. "The condition," he writes, "is evidently abnormal, but could have been construed as proof of a sexual relation between the spermogonium and aecidium by the older exponents of this view." Even more suggestive is Stahl's (1877) figure for *Physma compactum* of a vertical section of a spermogonium with trichogynes arising from the basal pseudoparenchyma and reaching the surface on both sides of the ostiole.

These hyphae also project from stomata in the vicinity of aecidia. Figure 5 shows one in front of a guard cell of the lower epidermis. It can be traced into the pseudoparenchyma below a young aecidium. The abrupt turn is characteristic of hyphae in this position. They seem to become part of the enclosing plechtenchyma of an aecidium. Possibly it is by this indirect approach that they reach the basal anlage of the aecidium. Figure 6 and the enlargements shown in figure 12, a-d, f, are drawn from a section containing two aecidia which have well developed spore chains but which have not broken the enclosing tissue. In one of the microscopic fields five groups of hyphae project from stomata on the under surface. These lie two to the left and three between the two aecidia. Blue-stained hyphae can be traced from these regions through the yellow-stained mass of hyphae which fills the substomatal regions and by the same difference in color they can be traced interruptedly into the plectenchyma of the aecidia. Bachmann (1912) has noted the same differential staining for the trichogynes of *Collema pulposum* in the lichen stroma. The above mentioned section was made from a leaf portion on which half-grown aecidia surrounded a group of old spermogonia. As one looks over the sections of this material one is impressed by the abundance of the hyphal tufts which

project from stomata. They occur near the spermogonia in positions which I have described above but they occur more abundantly on the under epidermis near the aecidia. They occur less frequently on the upper epidermis. Such an array of external hyphae would seemingly make very good respiratory organs as van Tieghem (1891) suggested for the trichogyne in *Polystigma*. However, de Bary (1887) disposed in summary fashion of that supposition and today the trichogyne of Stahl's *Collema* offers precedent for attributing a possible sexual function to these hyphae in the rusts. The tufted outgrowths also remind one of the clustered arrangement of trichogynes beneath the ostiole of the female conceptacles in *Epilithon*.

These finger-like tips of hyphae which push out through the stomata are apt to stain so densely with safranin that it is impossible to distinguish their cell contents. In the less densely stained tips a single nucleus is seen in the lower half of the finger-like hyphae. In figure 12, I have shown a series of studies of the occasional favorably stained hyphae. These are at higher magnification than the other figures. The dense nuclei or nucleoles of a, h, and left hand hypha of b and d were stained deep blue. The more diffuse nuclei, those of e and the right hand one of b stain red in a blue hypha. A more densely stained or differently stained tip can usually be distinguished on the pale-stained hyphae. This might indicate a secretion of some kind on the tip (fig. a, b). The wall usually takes the orange-G stain and such hyphae as the upper right hand one in figure e which lies at a lower plane shows merely as a pale yellow sac. There is great variation in the reaction of the hyphae to safranin and gentian violet but the more shrunken and probably older stages stain densely with safranin. Quite frequently the hypha is capped by a sphere which stains differently from the hypha. This, under favorable staining, shows a nucleus (figs. 6 and 12, a, b, c, e, f, and h). Figures 4 (right hand hypha), 7, 8, 9, and 12, g, show shrunken stages of the sphere. The profile views of 4 and 12, c and g, show a very slender connection between the sphere and the main hypha. I have arrived at no explanation of these structures, or of the red spheres of the same size that I have found occasionally on the leaf surface in the same smear with spermatia (fig. 10). Figure 12 of the hyphal tips, and figure 11, studies of spermatia taken from various groups, are drawn to the same magnification. It is to be noted that there is much variation in the size and shape of the spermatia. They are abstricted from the spermatophores as one-celled, oval spores, and both in the spermogonium and on the surface of the leaf show a nucleus clearly in the faintly stained cytoplasm. Cases are found of elongated spores and occasionally of a binucleate condition. The older spermatia which lie in masses at the ostiole of the spermogonium and are smeared over the leaf in the spermogonial exudate

are lens-shaped bodies which stain densely with safranin. There are, here and there on the leaf surfaces, cases where a spermatium seems to have germinated. In two different lots of material from leaves fixed a month after inoculation, on which both spermogonia and aecidia are erumpent, there are spores in the spermogonial exudate which have apparently budded out hyphae. In one case the tip of a hypha from the interior of the leaf has pushed up at one side of the ostiole of a spermogonium and lies in such a mass of spores.

I have found no convincing evidences of fusion between a spermatium and one of the hyphal tips although spermatia frequently lie close to the tips. As Klebahn (1904) has remarked, there need be no special significance attached to finding masses of spermatia in the stomatal depressions on a leaf which is dotted with spermogonia.

There are many cases of binucleate cells in substomatal hyphae (figs. 3, 6 and 14). Binucleate cells are also found in the pseudoparenchyma which encloses spermogonia. These did not show in the spermogonium of which figure 2 is a detail, but their occurrence in other of the spermogonial envelopes suggests a possible connection with the hyphal tips which so often penetrate stomata close to spermogonia. Figure 15 shows a binucleate condition in runners between cells of a palisade parenchyma. The hyphae at the top of this figure are from the base of an aecidium.

The aecidial anlagen develop in the spongy parenchymatous area of the leaf. Runners from between the palisade cells pass in interlaced plectenchymatous strands between the parenchyma cells to form the main mass of the young aecidium which can be recognized even in sections where the spermogonia are only just opening. Hyphae from the lower epidermal region may also enter such an anlage. In sections where the blue-stained mycelium stands out in contrast to the yellow-stained tissue of the leaf the pattern of these hyphae may be traced in curved lines from the lower epidermis to where they make up a large part of the pseudoparenchyma of the cup. From this periphery hyphae may be traced into the base of the aecidium. By such a path, hyphae whose tips project from stomata of the lower epidermis, below an aecidial anlage, may reach the base of the anlage. I have not been able to trace this course for any one hypha but the curve figured for the terminal hypha shown in figure 5 is characteristic for hyphae in these positions. The stoma of this figure is one from a lower epidermis and the hypha is embedded in a pseudoparenchyma which completely fills the area between epidermis and the peridium of an unopened aecidium. The hypha connected with one of the tuft of hyphae shown in figure 6 was embedded in a similar mass whose cells have not been drawn in. The hyphae shown in figures 2, 3, 4, and 8 were in the near vicinity

of spermogonia. The substomatal space in these cases is much more loosely filled with hyphae. Stomata occur on both surfaces of the *Oxalis* leaf; spermogonia are erumpent on both surfaces; with an occasional exception, aecidia open on the lower surface. If the fertilization path is by way of hyphae which extend from tips projecting from stomata to the anlagen of aecidia one would expect the upper leaf surface to be the more favorable position for the projecting tufts of hyphae. Hyphae project upon both surfaces of the leaf but it is an index of their greater frequency on the lower epidermis that the eight examples figured on plate 4, which were chosen merely for structural details, were all from the lower epidermis.

The hyphae which push between the parenchyma cells of the leaf to form the aecidial anlagen fork repeatedly in making the felted mass at the base of the aecidium. It thus becomes very difficult to follow any one strand but the sporogenous tissue stains generally a deeper red or blue than the other cells. Binucleate cells are seen early in the very base of the aecidium (fig. 15) while among them and above them multinucleate cells also appear early in the development of the anlage. I did not find evidences of Christman fusions. There are many fusions and occasional migrating nuclei between the irregular lobes of the crowded cells. See figures 21 and 22, drawn from adjacent sections of the base of a young aecidium (fifteen days after inoculation). One is especially conscious of the third dimension in looking at sections of this stage in the aecidium. Lobes project at different planes and a slight change of focus may bring into view a new fusion. Figure 22 shows a more vacuolate cell toward the base of the aecidium and denser cells with projecting lobes above. Figure 23 from a similar young aecidium shows another multinucleate cell with a lobe which is pushing up between other cells toward the upper part of the aecidium. Allen reports that the beginnings of the spore chains appear to be lobes from the multinucleate cells. Such an origin is indicated by the figures to which I have just referred and by figure 27. The latter is figured from an older stage of an aecidium and shows the very characteristic branching which interlaces the bases of the spore chains. One is reminded here of Richard's (1896) figure for an aecidium of *Uromyces Caladii* on *Peltandra*, "showing several points of origin of the hymenium." Figures 25 and 26 also show the branching origin of spore chains. Figure 24 from an older aecidium, where the spores are formed although the aecidium is not erumpent, shows the greatly lengthened and vacuolated basal cell of a chain (de Bary's basidium). De Bary's description (1887) gives still an excellent picture of the aecidium in its three dimensions. "The hymenium now makes its appearance at the base of the aecidium, on the flat surface which abuts on the surrounding mycelium; it is composed sometimes of an irregu-

larly shaped, but much more usually of a circular and continuous layer of short cylindrically club-shaped basidia directed vertically towards the apex; each basidium abjoins a single long row of spores in basipetal succession one after another with temporary intermediate cells."

The development of the aecidium of *Aecidium punctatum* is, according to my observations, very similar to that of *Puccinia Sorghi*. In the aecidium binucleate cells occur regularly in the basal tissue. There are instances here also of migrating nuclei. I have not, however, found this in the higher region of the basal cells of spore chains. The spermogonia of *Aecidium punctatum* are subcuticular. In their formation, hyphae push up between the epidermal cells and grow in the cutin toward a common point. In sections of spermogonia the remnants of these closely woven hyphae can be seen in the red-stained cutinous cap over the hemispherical spermogonium. There are few paraphyses and these slant as a thatch toward the top of the spermogonium. Under this thatch from a layer of basal cells just outside the host epidermis an upright growth of spermatophores develops. The spermatia which are successively abstricted, discharge in great numbers through the central hole in the thatch of paraphyses. The latter do not project from this ostiole. Spermatia are found abundantly in the sections, on the surface of the leaves but, since the amphigenous stomata of the *Hepatica* leaf are not located in depressions as in *Oxalis*, there is no particular massing of spermatia around stomata. In this rust hyphae do not project through stomata according to my observations. In comparison with *Puccinia Sorghi* the absence of any projecting tufts is marked on sections of leaves containing spermogonia and aecidia of approximately the same age as those of *Oxalis* from which figures 2-12 were made. I did find, however, many instances of hyphal tips just below or within the stoma (fig. 19) and of hyphal tips which had pushed up between epidermal cells and run horizontally in the cutin. A binucleate condition is frequent in these cells. Binucleate cells and migrating nuclei are found in the mycelium around the spermogonia.

DISCUSSION

As reported above, I have found in *Puccinia Sorghi* upon *Oxalis* much the same structures which Allen (1932) reports for *Puccinia trititina* upon *Thalictrum*. (These hyphae which push out through stomata may be trichogynes, but I lack the proof of fusions between these hyphae and spermatia.) Except for Craigie's evidence that spermatia function in the production of aecidia and for our further knowledge of nuclear distribution in the hyphal cells, the matter stands as it did in the time of de Bary when he considered the evidence was insufficient to warrant calling the hyphae

trichogynes. The hypothesis offers another possible explanation for the substomatal hyphae which Clinton (1919) describes for *Cronartium ribicola* in the needles of *Pinus Strobus*. Clinton believes that sporidia of this rust, contrary to the usual habit of sporidia, enter through the stomata of the host. He has not found the entering germ tubes but he finds, in substomatal spaces of infected leaves, a vesicle from which a hypha leads to the intercellular spaces and from which a short beak projects between the guard cells. He considers the vesicle "to be an inflation of the germ tube immediately it has passed the guard cells into the air chamber" but in his figure 6, plate 43, the hypha is sufficiently like some which I have found to suggest that it might be growing out instead of in. Clinton, however, does not report any binucleate hyphae and he finds no trace of penetrations through epidermal cells as I have in *Oxalis*. The fact that these hyphae in the case of *Aecidium punctatum*, do not appear to push out through stomata but directly between epidermal cells, need not necessarily be evidence against their functioning as trichogynes. The binucleate hyphae between epidermal cells and in the cuticle may serve this same function but this difference in structure and habit should make one realize that there is much yet to be seen before we may talk confidently of trichogynes in connection with the rusts.

I did not find the multinucleate condition in trichogyne-like cells, as reported by Allen (1932) for *Puccinia trititica*, in any of the rusts which I investigated but until further observations are available it is perhaps unnecessary to consider this point further. In the matter of the aecidial anlage there is also need of much more observation. Conditions observed in *Puccinia trititica* and in *Puccinia Sorghi* certainly suggest that the nuclear conditions reported by earlier workers as abnormalities or exceptions to the method of the initiation of spore chains by the Blackman or Christman types of fusion are to be further studied.

The reports which I have seen in the literature, of Blackman and Christman fusions made by sixteen workers from 1904 to 1927 show fusions for nineteen rusts of the caeoma type and twenty-four of the peridium type. One cannot therefore regard the phenomenon as a caeoma type character even though it is in the peridium type that recent investigators fail to find them. The figures from these publications vary greatly in the value of their evidence for fusions. Several of the students in this list mention the apparently sporadic occurrence of binucleate cells below the fusion cells. Allen lists five instances of sporophytic mycelium mingled with gametophytic as reported in the literature. The earliest is that of Blackman and Fraser who report that in *Puccinia Poarum* "paired nuclei were also to be observed at a stage before the differentiation of the fertile layer

or in cells below that layer after its differentiation." It may be that these cases are really nothing more than the early occurrence of binucleate cells which I found to be a regular occurrence in both *Oxalis* and *Hepatica* rust.

Andrus (1931) mentions cases in the bean rust where nuclei were found passing through the cross walls of hyphae which enter the aecidium and migrating into the fertile cells of the aecidium. He interprets this as an evidence of fertilization from trichogenous hyphae above. The matter is of course conjecture at present but it is open to question whether these cases may not be part of the cell fusion phenomenon which I have found, in the *Oxalis* rust, linked up apparently with the occurrence of multinucleate cells. The cases of nuclear migration which I found in both *Oxalis* and *Hepatica* rust were located in the base of the aecidium.

Allen (1930, 1932) does not discuss the possibility that the multinucleate cells of the young aecidium may arise by cell fusions. Such an occurrence would have at least the support of comparative morphology. The formation of coenocytic cells by fusions is a part of the post-fertilization process in the development of carpospores in the red algae. The Christman fusions have been compared by Dodge (1926) to the auxiliary cell fusions in the red algae. *Dudresnaya*, upon the authority of Oltmanns (1922), is now a classic case for successive fusions between gonimoblasts and auxiliary cells. For comparison with the aecidial fructification the isolated carposporic masses of *Dudresnaya*, which arise where each new length of gonimoblastic filament fuses with an auxiliary cell, may be telescoped into one fruit. This condensation of many cystocarps into a single conceptacle occurs in the Corallinaceae. In this group antheridia, carpospores and tetraspores all develop as aggregates in conceptacles. Nichols (1908) has described the process of carpospore formation in certain Corallines of the Pacific coast. Although he gives no cytological data he describes and figures the carpospores in the cystocarpic conceptacle for three species of *Lithophyllum* and for *Lithothamnium marginatum* as arising from a large coenocytic basal cell. He writes: "A disk-shaped placenta occupies the base of the conceptacle around the periphery of which the carpospores occur." Kylin (1928) traces the development of the cystocarpic conceptacle in *Epilithon membranaceum* showing that it involves the formation of a gigantic coenocytic cell by the fusion of gonimoblasts and auxiliary cells. From the floor of the young conceptacle rows of upright cells arise. In the central group are three-celled carpogonial branches, tipped with trichogynes. Around them stand two-celled auxiliary cell branches. After fertilization the carpogonium fuses with the first cell of a carpogonial branch but not necessarily with a cell of its own branch. From the resulting fusion cells gonimoblasts develop which fuse with basal cells of the aux-

iliary branches. Kylin concludes: "Im Schlusstadium beobachtet man indessen, dass alle Auxiliarzellen und Nährzellen, sie mögen in den Karpogonästen oder in den Auxiliarzellästen auftreten, miteinander zu einer grossen Fusionszelle verschmolzen sind . . . Aus dem Rande der Fusionszellscheibe entwickeln sich mehrere zwei-bis dreizellige Fäden, deren oberste Zellen Karposporen bilden."

Surely this multinucleate cell may serve as a prototype for aecidial development in which multinucleate cells are reported in the primordium, yet Allen does not discuss this possibility.

The nuclear problem, however, is by no means solved by an *Epilithon* prototype. The behavior of the nuclei in the red algae with the nucleus of the auxiliary cell remaining in the far corner of the fusion cell and the diploid nucleus alone continuing in gonimoblasts and carpospores seems clear on an Oltmann chart for *Dudresnaya* or *Calithamnion*. Still the nuclear behavior has not been worked out for *Epilithon*. A confirmation of Oltmann's (1922) claim as to the fate of the auxiliary cell-nuclei is very much needed.

The evidence brought by Rosenvinge (1929) that in *Phyllophora Brodiaei* the reduced sporophyte is in permanent nutritive relations with the haploid gametophyte might indicate an extension of such a purely nutritive function of auxiliary cells with the disappearance of the diploid carposporic stage. Rosenvinge reports for this species that although there are antheridia and procargs on the same plants no spermatia are seen upon the aborted trichogynes and there are no other signs of fertilization. Nevertheless the "bearing cell" at the base of the procarg, originally uninucleate, becomes plurinucleate and sends out protuberances. These force their way between the cells of the gametophytic tissue but instead of developing carpospores as do the gonimoblasts of the related species, *Phyllophora membranifolia*, they form, on this gametophytic plant, low, wart-like structures similar to the nemathecia of the diplobiontic *Phyllophora membranifolia* and, as it would seem to me, morphologically comparable to the uredo-teleuto mycelium and spores in the rusts. Here again Ruth Allen (1930) might have found a suggestive similarity with the multinucleate cells of the aecidium as they "push down into the sterile 'space-making' tissue of the aecium to produce spore chains." In the nemathecium, within an outer portion of radiating filaments, there is a medullary tissue of rounded cells which develop typical tetraspores. The nuclear condition of the tetraspores has not been investigated but it is seemingly complicated by connections between fertile cells in contiguous rows as well as the usual ones within each row. Rosenvinge remarks "It would be of interest to study the fate of the migrating nuclei in this process."

Rosenvinge has germinated these tetraspores of the nemathecium and obtained from them small thalli which resemble young stages of *Phyllophora Brodiaei*. The nemathecium are thus proved to be part of the life-cycle of *Phyllophora* rather than a parasite. Rosenvinge states that a closer cytological investigation needs to be made but he believes that in this species the carposporophytic phase has disappeared and in its place a tetrasporophyte is developed whose vegetative part is only represented by the intramatrical cell-filaments imbedded in the haploid tissue of the parent gametophyte. The importance of this simplified condition of the sporophyte lies in the fact that *Phyllophora* belongs to that group of the red algae which Svedelius (1931) calls the *Polysiphonia* type: a typical diplobiont with morphological alternation of generations and reduction division at the time of tetraspore formation. The shortening of the diploid generation without losing the advantage of multiplication by spores as seen here is, Svedelius (1931) thinks, carried to a climax of simplification in *Ahnfeltia plicata* where, as reported by Rosenvinge (1931), nemathecium are the only reproductive organs known. Rosenvinge has followed the development of these spores and emphasizes their multiple origin from a layer of generative cells in the nemathecium. He thinks that these generative cells may be reduced procarps and that the whole complex of cells arising from the generative cells must be considered as representing a new generation comparable to the sporophytic generation in *Phyllophora Brodiaei*. This theory raises questions concerning nuclear conditions and chromosome numbers which require further cytological work but it certainly suggests a comparison with the multiple origin of the aecidiospore chains in the aecidium cup.

There are cases among the reduced Ascomycetes which parallel closely the conditions in the autotrophic *Phyllophora*. We have cases, where, as reported by Fraser, there is a degeneration of sexual organs and, consequently no fertilization but where the asci still develop. In *Lachnea stercorea* (Fraser, 1907) although the antheridium fuses with the trichogyne its contents are said not to travel to the oogonium. Nevertheless the nuclei of the oogonium increase in number, fuse in pairs and these fusion nuclei supply the ascogenous hyphae. In *Lachnea cretea* (Fraser, 1913) there is a branched trichogyne but no antheridium has been observed. Nevertheless, in the central part of the archicarp the septa break down and ascogenous hyphae arise from the resulting multinucleate fusion cell. In *Humaria rutilans* (Fraser, 1908) reduction has gone still further; sexual organs are completely lacking and ascogenous hyphae arise from cells which contain fusion nuclei. There seems to be a parallelism in the basic facts of spore development between the rusts, the Ascomycetes, and their possible an-

cestors, the red algae. If functioning trichogynes as well as spermatia are now to be looked for in the rusts one may expect to find a *Polysiphonia* type, but there are many variants to be fitted in.

Dodge (1924) has reported three races of the short cycled form of *Caeoma nitens*: one a male race with spermogonia but with uninucleated aecidiospores producing two-celled promycelia; second, a female race with spermogonia lacking and uninucleated aecidiospores producing two-celled promycelia; a third hermaphroditic race with spermogonia present and binucleated aecidiospores producing four-celled promycelia. Dodge (1932) has described these as "androgenetic, parthenogenetic, and syngamic (hermaphroditic) races." With the steps in the process which initiates the sporophytic generation in the rusts still not clear, there is, nevertheless a possible parallelism between the hermaphroditic race of *Caeoma nitens* and *Phyllophora Brodiaei*, and between the uninucleate races of *Caeoma nitens* and the simplified type of *Ahnfeltia plicata*.

Suggestive as such comparisons are as a help toward explaining reproductive processes in the rusts it should be remembered that the nuclear problem, (assuming that Oltmann's account of the nuclear behavior in the so-called secondary and tertiary fertilizations of *Dudresnaya* is true), is a very different one in the rusts as compared with the red algae and the other great parasitic group, the Ascomycetes. In the rusts conjugate nuclei are the accepted fact of the diploid generation. The rusts belong, moreover, to the line of Basidiomycetes which, by means of the clamp connection mechanism, insures the perpetuation of a line of non-sister nuclei. Thus comparisons with the red algae where the diploid nucleus is so far as known, single, as compared with the rusts where conjugate nuclei are present in the diplont; and with the Ascomycetes where the crozier offers a still different method for sorting out nuclei still leave many problems to be cleared up.

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Description of plates 4-6

The figures of plates 4-6 were drawn with the aid of a camera lucida from sections 5-7.5 microns thick. For figs. 1-9 and 13-27 a Zeiss apochromatic objective 4 mm. and compensating ocular 15 \times were used, with approximate magnification $\times 1200$; for figs. 10-12 a 1/16 inch oil immersion objective and an ocular 15 \times were used, with approximate magnification $\times 1800$. The following fixations were used:

Figs. 16-20.....	Flemming's medium solution
Figs. 12g, 19, 24, 25.....	Flemming's weak solution
Figs. 1, 3, 4, 8-10, 12e, 13-15, 21, 22, 27.....	Allen's B-15 solution
Figs. 6, 12a-d, f, h, 26.....	Carnoy's solution
Figs. 2.....	50% alcohol
Figs. 5, 7.....	Corrosive sublimate in 70% alcohol

The material was stained in Flemming's triple stain.

PLATE 4

Puccinia Sorghi in *Xanthoxalis stricta*

Fig. 1. An infection hypha in a cell of the upper epidermis near a spermogonium.

Fig. 2. Short branches from hyphae at the border of a spermogonium, projecting from a stoma of the lower epidermis.

Fig. 3. A hyphal tip protruded from a stoma. Binucleate hyphae in the substomatal space.

Fig. 4. A group of hyphae at a stoma showing their independent origin from substomatal hyphae. The external depression in which the stoma lies is filled by a mass of spermatia in the spermogonial exudate.

Fig. 5. A hypha lying in a mass of pseudoparenchyma which fills the space between lower epidermis and an aecidium. The tip of the hypha projects against a guard cell of a stoma.

Fig. 6. A tuft of hyphae projecting from a stoma. The dense hyphae are stained red, the others are pale blue with deep blue nuclei. The pseudoparenchyma in which the substomatal hypha is embedded has been omitted. The hypha extends in the direction of an aecidium.

Fig. 7. A shrunken, blue-stained hyphal tip which has pushed out between companion cell and guard cell of a stoma; in the same microscopic field as fig. 5.

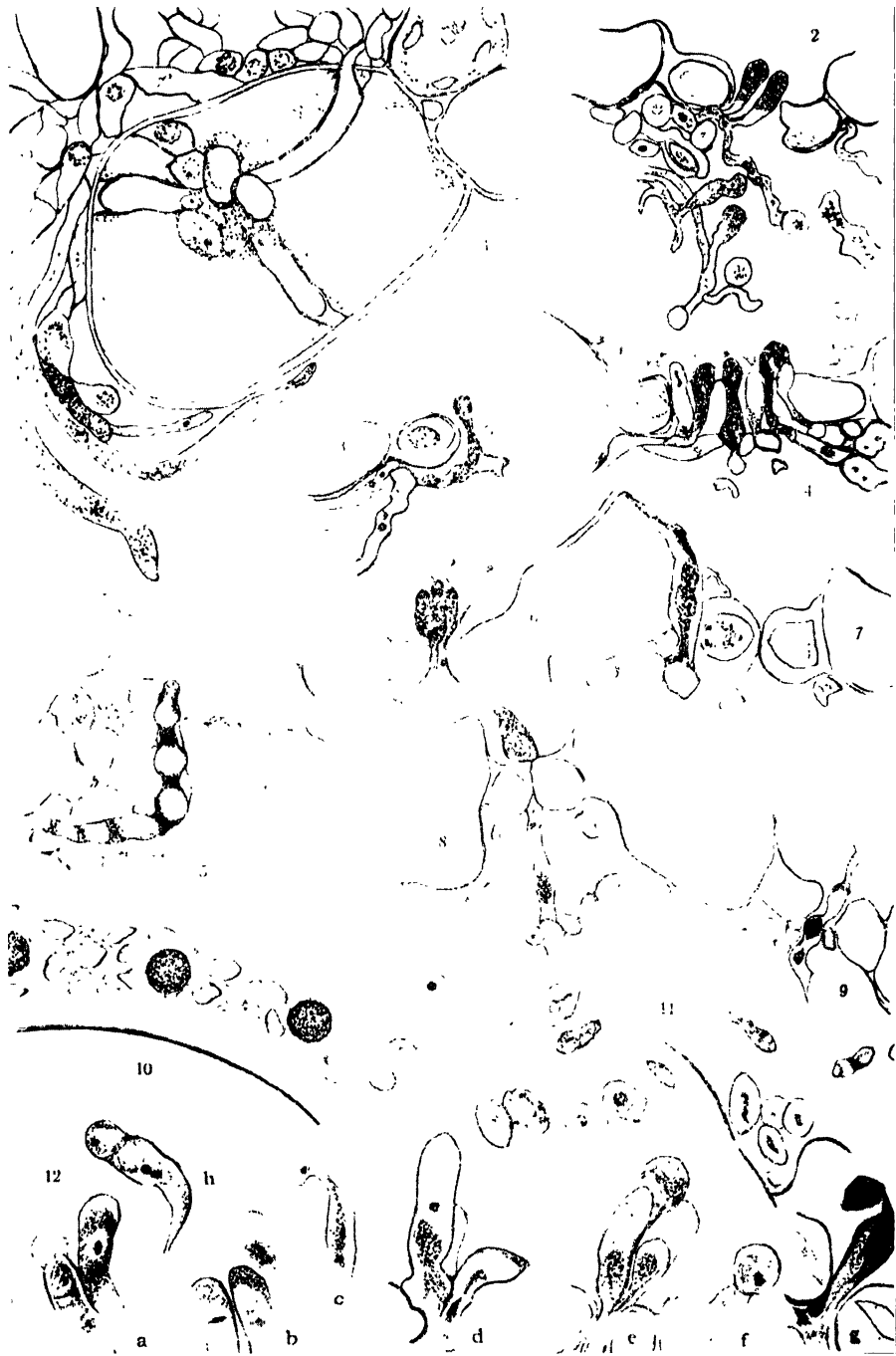
Fig. 8. A substomatal hypha with a dense, red-stained tip projecting above a stoma into the depression between the two companion cells. The stoma is near a spermogonium.

Fig. 9. A shrunken hyphal tip projecting from a stoma; from the same section as fig. 8 but below an aecidium.

Fig. 10. Red-stained spheres in a smear of spermatia upon a leaf surface; near the tuft of projecting hyphae shown in fig. 12, e.

Fig. 11. Spermatia drawn from groups found on the leaf surfaces in the vicinity of spermogonia. The dense nucleus at the upper left is red-stained; the others are blue. The three at the upper right are of the type from which, in three cases, germinating hyphae had issued. These were found each time in spermatial masses at the ostioles of spermogonia.

Fig. 12. Tips of hyphae which protruded through stomata; drawn to the same magnification as figs. 10 and 11.



RICE REPRODUCTION IN RUSTS

- a. A group from a hypha on the same epidermis as fig. 6.
- b. A group from the same section as fig. 12, a. The hyphae are stained blue; the left hand nucleus, blue, and the right hand nucleus, red. The terminal sphere is stained yellow with red contents.
- c. Detail of the hypha which is at the lower plane in fig. 12, d. A terminal sphere is shown in profile.
- d. Another group from the same section as fig. 6.
- e. A group of hyphae from the same section as figs. 8 and 9. Two pale yellow hyphae which lay at an upper level have been omitted from the figure.
- f. Enlargement of right hand hypha from fig. 6.
- g. An old hypha with dense, red-stained contents and profile view of a spherical tip. Both aecidia and spermogonia are near the stoma.
- h. A hypha from a stomatal group from the same section as fig. 6.

PLATE 5

Puccinia Sorghi in *Xanthoxalis stricta*

Fig. 13. Paraphyses and protruding hyphae at the ostiole of a spermogonium.

Fig. 14. A hypha with binucleate cells in a substomatal space.

Fig. 15. Binucleate hyphae between palisade cells. The hyphae in the upper part of the figure are in the anlage of an aecidium.

Puccinia Violae in *Viola cucullata*

Fig. 16. Binucleate hyphae in front of a guard cell of a stoma on the upper epidermis: possible infection hyphae from aecidiospores.

Fig. 17. Binucleate hyphae at a stoma in another section of a violet leaf.

Fig. 18. A short hyphal branch protruding from a stoma. The cell below is a cross section of the runner from which the hypha arises.

Aecidium punctatum in *Hepatica acutiloba*

Fig. 19. A substomatal hypha with its tip between two guard cells.

Uromyces Caladii in *Arisaema triphyllum*

Fig. 20. A terminal hypha in a stoma. A spermatium lies at the surface of the guard cell.

PLATE 6

Puccinia Sorghi in *Xanthoxalis stricta*

Fig. 21. Detail from the base of a young aecidium in a 15 day-old infection.

Fig. 22. Detail from the next section of the same aecidium as that of fig. 21.

Fig. 23. Multinucleate cells from a young aecidium.

Fig. 24. A "basidium" from an aecidium in which the spore chains are formed.

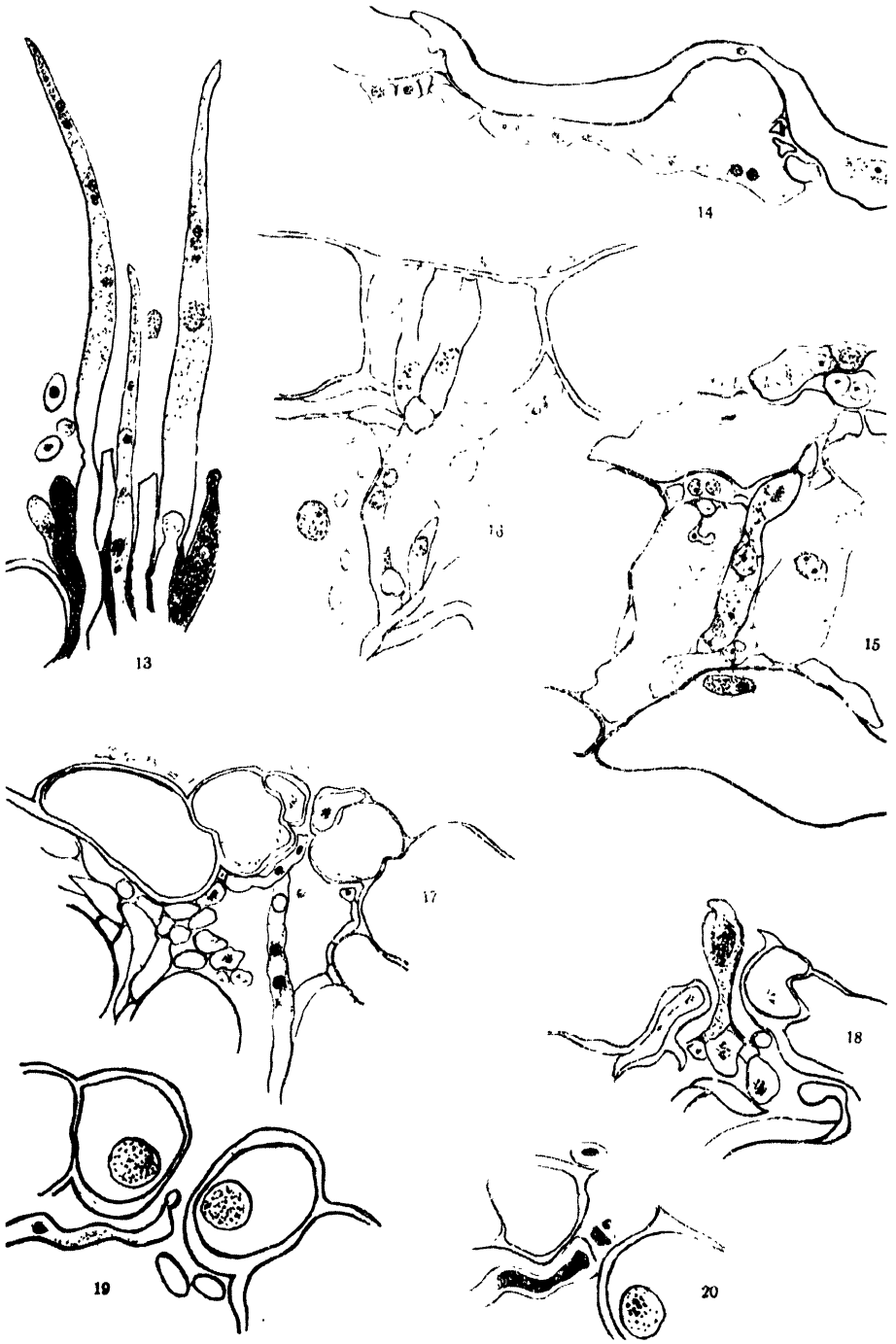
In figs. 21-24 the upper part of the figure is toward the upper surface of the leaf. The aecidium is developing toward the under surface.

Fig. 25. An intermediate stage between figs. 23 and 24, showing branching origin of spore chains.

Fig. 26. A stage of the "basidium" younger than that of fig. 24.

Fig. 27. Vertical section of the anlage of an aecidium.

In figs. 25-27 the position of the cells is the reverse of figs. 21-24.



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RICE REPRODUCTION IN RUSTS

Nomenclatural notes

HAROLD N. MOLDENKE

Callicarpa Merrillii Moldenke, nom. nov.

In reviewing the literature on the verbenaceous genus *Callicarpa* in connection with a monograph of the American members of this genus which is at present in preparation, it was discovered that the name *Callicarpa lancifolia* proposed by Merrill in 1915 (Philipp. Jour. Sci. Bot. 10: 70) for a new Philippine species of this genus, is a homonym of the earlier *C. lancifolia* Millsp. (Publ. Field Columb. Mus. Bot. 2:312.1909) and is therefore invalid. The Philippine species, the type of which was collected by Maximo Ramos (Philipp. Bur. Sci. No. 11,078) on the island of Cebu in March, 1912, must therefore be given a new name, and for it the new binomial *Callicarpa Merrillii* is hereby proposed. It is indeed most fitting and proper that this specific name be applied to the plant in question, in commemoration of Dr. Elmer Drew Merrill, who first recognized it as a new species, and who has done such extremely noteworthy work on the Asiatic flora and more especially on that of the Philippine Islands. *C. Merrillii* is apparently closely related to *C. stenophylla* Merr. and *C. longifolia* Lam., and is known also from the islands of Mindoro, Ticao, Mindanao, and Basilan. The type of *C. lancifolia* Millsp., on the other hand, was collected by Charles Wright (No. 3173) in eastern Cuba between the years 1860 and 1864. The latter—a very distinctive and endemic Cuban species—will be fully discussed in the writer's forthcoming monograph.

CALLICARPA NUDIFLORA Hook. & Arn.

It has also been found through a study of the literature on this extremely interesting genus that the Asiatic plant hitherto known as *C. acuminata* Roxb. must take on a new name. It is true that the name *C. acuminata* was first proposed by Roxburgh for this Asiatic species (Hort. Beng. 10. 1814), but without any description. Being therefore a hyponym, it was not validly published at this date. A full description of his *C. acuminata* was not published by Roxburgh until 1820 (Fl. Ind. 1:394). In the meantime, however, Humboldt, Bonpland, and Kunth published their Central and South American *C. acuminata* (Nov. Gen. & Sp. Pl. 2:252. 1817) and accompanied the name with a full description. The Asiatic and American plants are not conspecific. The American plant, therefore, must retain the name *C. acuminata* H.B.K. given to it in 1817 because Roxburgh's use of the name in 1814 was not valid publication; and Roxburgh's Asiatic species must take on a new name. The second oldest name for this Asiatic species is *C. Reevesii* of Wallich (Cat. no. 1830. 1829), but

this also is a mere hyponym. The name *C. Reevesii* Wall. was not validly published until by Walpers in 1845 (Rep. Bot. Syst. 4:125). In 1836, however, Hooker & Arnott published *C. nudiflora* (Bot. Beech. Voy. 206) with a good description and illustration. It is therefore obvious that this Asiatic species first known as *C. acuminata* Roxb. and then as *C. Reevesii* Wall. must now be called *C. nudiflora* Hook. & Arn. It has been collected rather extensively in south China, Canton, Kwantung, Hainan, Macao, and Lappas Island, and occurs also in Silhet, Tenasserim, and Singapore.

***Celeri graveolens* var. *dulce* (Mill.) Moldenke, comb. nov.**

***Celeri graveolens* var. *rapaceum* (Mill.) Moldenke, comb. nov.**

The generic name *Celeri* of Adanson (Fam. Pl. 2:498. 1753) is maintained by Britton and others for the six or more species of *Apium* which are characterized by having white flowers and oval fruit. The true genus *Apium*, then, according to this view, is limited to the twenty or more species with yellow flowers and hemispheric fruit. Since the genus *Celeri* has thus been accepted, with the common celery (*Apium graveolens* L.; *Celeri graveolens* [L.] Britton) as the type species, it is obvious that the two common garden varieties of this species known respectively as the upright celery and the celeriac must likewise be transferred to this genus. The combination *Celeri graveolens* var. *dulce* is therefore hereby proposed for the *Apium dulce* of Miller (Gard. Dict., ed. 8, no. 5. 1768)—a plant which has likewise been called *Apium Celeri* by Gaertner (Fruct. & Sem. 1, t. 22. 1788) and *Apium graveolens* var. *dulce* by De Candolle (Prodr. 4:101. 1830)—and the combination *Celeri graveolens* var. *rapaceum* for the *Apium rapaceum* of Miller (Gard. Dict., ed. 8, no. 6. 1768), which is the *Apium graveolens* var. *rapaceum* of De Candolle (Prodr. 4:101. 1830).

***Cynoxylon floridum* var. *pendulum* (Dipp.) Moldenke, comb. nov.**

***Cynoxylon floridum* var. *rubrum* (André) Moldenke, comb. nov.**

Since the flowering-dogwoods, which are distinguished by being trees or shrubs with capitate flowers involucrate by four large white or colored bracts, are by many modern authorities kept distinct, as the genus *Cynoxylon* Raf. (Alsog. Amer. 59. 1838), from the ordinary dogwoods or cornels which make up the genus *Cornus* L. (Sp. Pl. 117. 1753) proper and which are distinguished by their cymose and non-involucrate inflorescence, then it is obvious that the two common horticultural varieties known respectively as the weeping flowering-dogwood and the red flowering-dogwood must be renamed. Being varieties of the *Cornus florida* of Linnaeus which is now more properly called *Cynoxylon floridum* (L.) Raf., they also must be transferred to the genus *Cynoxylon*. This has apparently not been

done up to the present time. The combination *Cynoxylon floridum* var. *pendulum* is therefore hereby proposed for the *Cornus florida* var. *pendula* of Dippel (Handb. Laubh. 3:244. 1893) and the combination *Cynoxylon floridum* var. *rubrum* for the *Cornus florida* var. *rubra* of André (Rev. Hort. 66:500. 1894).

Pleuropterus sachalinensis (F. Schmidt) Moldenke, comb. nov.

The name *Pleuropterus* was proposed as a genus of the *Polygonaceae* by Turczaninow in 1848 (Bull. Soc. Nat. Mosc. 21¹:587). Recent workers on this family, like Steward, have reduced the name to sectional rank under the genus *Polygonum* or have united it with *Tiniaria*, while others, like Small and Nakai, have retained it as a valid genus. The characters distinguishing members of the genus *Pleuropterus* from all other members of the *Polygonaceae*, as given by Small in a key to genera in Britton & Brown's "Illustrated Flora" (ed. 2, 1:647. 1913), are as follows: Plants with fibrous roots or slender rootstocks, without scaly caudices; stems branching; leaves not basal, their blades not jointed; ocreae oblique, not 2-lobed, but more or less open on the side facing the leaf; inflorescence branched; sepals, at least the outer ones, keeled or winged; filaments slender; stigma dilated, toothed; styles divaricate. In the opinion of the present writer, *Pleuropterus* ought certainly be retained as a valid genus, since its members are so distinct in their technical characters and in their habit and general appearance and are so easily recognized. The *Polygonum sachalinense* of F. Schmidt (Maxim., Prim. Fl. Amur. 233. 1859), then, must be transferred to this genus. The name *Pleuropterus sachalinensis* is therefore hereby proposed for this plant. This genus, then, to date contains four species, all natives of eastern Asia, although the second is locally naturalized in the eastern United States: (1) *Pleuropterus multiflorus* (Thunb.) Turcz.—first named *Pleuropterus caudatus* by Turczaninow and made the type of the genus, but since this name was confessedly only a new binomial for the *Polygonum multiflorum* of Thunberg (Fl. Jap. 1:169. 1784) it was later corrected by Turczaninow himself to *Pleuropterus multiflorus* (vid. Nakai in Fedde, Repert. 13:267. 1914), which, obviously, is the name which will have to be adopted for this species; (2) *Pleuropterus Zuccarinii* Small (in Britton & Br. Ill. Fl., ed. 2, 1:676. 1913); (3) *Pleuropterus ciliinervis* Nakai (in Fedde, Repert. 13:267. 1914); and (4) *Pleuropterus sachalinensis* (F. Schmidt) Moldenke (the *Polygonum sachalinense* of F. Schmidt).

Viorna albicoma (Wherry) Moldenke, comb. nov.

Since the thirty or more species of leatherflowers, which are characterized by their erect or ascending stems, their mostly solitary flowers, and

their more or less converging sepals, are usually kept distinct as the genus *Viorna* of Reichenbach (Handb. 277. 1837)¹ from the approximately similar number of species of virginsbowers which compose the true genus *Clematis* of Linnaeus (Sp. Pl. 543. 1753), and which are distinguished from the above by their spreading sepals and stamens and their paniced flowers, then the *Clematis albicoma* of Wherry (Jour. Wash. Acad. Sci. 21:198, fig. 1. 1931) must be transferred to this genus. The combination *Viorna albicoma* is therefore hereby proposed for this rare Virginian and West Virginian plant.

***Vitex tomentulosa* Moldenke, sp. nov.**

Frutex; ramulis gracilibus obtuse tetragonis densissime et breviter brunneo-tomentulosis glabrescentibus; internodis valde abbreviatis; cicatricibus foliorum delapsorum plerumque conspicuiter impressis; foliis oppositis trifoliolatis; petiolis gracillimis densissime et breviter tomentulosis; petiolulis ad 1 mm. longis vel nullis dense tomentulosis; foliolis 3, medio subcoriaceo anguste lanceolato longe acuminato revoluta ad basin cuneato et in petiolulum attenuato, supra minutis resinosis globulis vel lepidibus dense oblecto, subtus densissime brunneo-tomentuloso; foliolis lateralibus medio consimilibus sed paulum parvioribus; inflorescentiis axillaribus paniculatis; pedunculis gracillimis densissime et breviter tomentulosis; cymis ut videtur in quaque panícula 5 parvis, infernis oppositis, quoque jugo a bracteis linearibus 2 subtento; bracteis utrinque dense tomentulosis; bracteolis et prophyllis numerosis linearibus tomentulosis; calicis obconico-campanulati plusminus 4-5-angulati densissime granuloso-pulverulenti limbo subtruncato ad apicem angularum vix vel paulo 4-5-dentato; corollae infundibulariformis vel hypocateriformis tubo late cylindrico intus plusminus dense piloso, lobis 4 oblongo-lingulatis paulum inaequalibus latissime rotundatis puberulentibus, extra leviter granuloso-pulverulentis; staminibus 4 prope os tubae corollae insertis; filamentis pilosis; stylo glabro; stigmate bifido.

Shrub; branchlets rather slender, grayish, obtusely tetragonal, very densely short-tomentulose with brownish tomentum, becoming glabrate in age; internodes much abbreviated, usually 4-6 mm. long at the tips of the branchlets; leaf-scars usually conspicuously impressed; leaves decussate-opposite, trifoliate; petioles very slender, 2.5-5.5 cm. long, flattened and conspicuously canaliculate above, very densely short-tomentulose; petiolules extremely short (or absent), to 1 mm. long, flattened and deeply canaliculate above, densely tomentulose; leaflets 3, the terminal one subcoriaceous, narrow-lanceolate, 4-6.5 cm. long, 8-15 mm. wide, long-acuminate at apex, revolute along the margins, cuneate at the base and attenuate into the petiolule, densely covered with minute resinous globules or scales above, less so in age,

¹ This name was apparently first proposed [as a section of *Atrogene*] by Persoon in his "Synopsis Plantarum" (part 2; p. 98. 1807). The generic name is on this account inaccurately accredited to him by Reichenbach.

very densely brownish tomentulose beneath with extremely short appressed scurfy tomentum; midrib deeply impressed above, very prominent beneath; secondaries about 8 pairs, short, ascending, impressed above, prominent beneath; lateral leaflets similar in all respects to the terminal one only slightly smaller; inflorescence axillary, paniculate, 3-5 cm. long (in bud); peduncles very slender, 1.5-3 cm. long, very densely short-tomentulose; cymes apparently about 5 in each panicle, small, the lower ones paired, to about 1 cm. long, each pair subtended by 2 linear bracts which are to 1 cm. long and densely tomentulose on both surfaces; bractlets and prophylla numerous, linear, tomentulose; calyx obconic-campanulate, about 2.8 mm. long and 2.6 mm. wide, somewhat 4-5-angled, subtruncate, scarcely or very slightly 4-5-toothed on the angles, very densely granulose-pulverulent; corolla infundibular or hypocrateriform, its tube broadly cylindric, about 2.3 mm. long, very much ampliate above, more or less densely pilose within, its limb 4-parted, slightly irregular, its lobes broadly oblong-lingulate, 1-1.3 mm. long and wide, very broadly rounded at apex, puberulent, slightly granulose-pulverulent on the back; stamens 4, inserted near the mouth of the corolla-tube; filaments filiform, about 1.3 mm. long, pilose; anthers oblong, about 0.6 mm. long and 0.3 mm. wide; style capillary, 2-3 mm. long, glabrous; stigma bifid, its branches about 0.5 mm. long, erect, somewhat divergent; ovary subglobose, about 0.7 mm. long and wide, somewhat tetragonal, granulose-pulverulent on the top; fruiting-calyx and fruit not seen.

The type of this interesting species was collected by A. Fors [*Juan T. Roig 5831*] at Los Yayales Remates de Guane, Pinar del Rio, Cuba, on March 25, 1929, and is deposited in the herbarium of the New York Botanical Garden. A vernacular name for this plant, according to its collector, is "Robleguiro." The species is very distinct and quite different from all other known West Indian species.

***Xanthoxalis corniculata* var. *atropurpurea* (Planch.) Moldenke, comb. nov.**

Since the generic name *Xanthoxalis* of Small (Fl. SE. U. S. 666. 1903) is now applied to the fifty or more species of yellow-flowered caulescent woodsorrels, the common horticultural variety known as the purple-leaved yellow woodsorrel must likewise be transferred to this segregated genus. The combination *Xanthoxalis corniculata* var. *atropurpurea* is therefore hereby proposed for the *Oxalis corniculata* var. *atropurpurea* of Planchon (Fl. Serres 12:47. 1857). This variety has been found by the present writer to persist quite extensively after cultivation and often becomes quite weedy. It will frequently be met with as an escape around old gardens and in waste ground.

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE

1930-1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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A *Protolepidodendron* from the Devonian of Virginia

EDWARD W. BERRY

(WITH PLATE 7)

There came into my hands during the past summer a small collection of plant material from the Devonian at an exposure $3\frac{1}{2}$ miles west of Covington, Virginia, and just west of a road-pass bridge over the Chesapeake and Ohio Railroad right of way. At this locality there is a considerable thickness of littoral or continental beds which lie near the boundary between the middle Devonian Romney formation and the upper Devonian Jennings formation.

This collection was made by Brinton H. Stone, who is making a study of the Devonian of that region. The collector is inclined to refer the plant horizon to the top of the Romney rather than to the base of the Jennings because it lies some distance beneath a dark fissile shale similar to one which in the Maryland region is referred to the Genesee member of the Jennings. It may be said that the lithologic and to a considerable but much less extent the paleontologic expression of the middle and upper Devonian from Maryland southward differs from the New York standard section, so that it has not been possible to recognize the numerous formational units of the latter with any degree of precision, although there is sufficient paleontologic evidence in the southern region to show that the Romney formation (Darton 1892) represents the time of the Onondaga, Marcellus and Hamilton of the New York section, and that the Jennings (Darton 1894), at least in Maryland, with its four members, represents all or in part the Genesee, Ithaca, Portage and Chemung of the New York section.

It is *a priori* highly improbable that the recognized members of the Devonian in Maryland and the Virginias with their varying lithology and thicknesses are the exact equivalents of the formations with which they are correlated in New York, and there is a certain amount of field evidence that such is not the case. This brief resume will serve as an introduction to an account of the most interesting plant fossil from near Covington, Virginia, which is a considerable cortical fragment of what White described¹ in great detail in 1907 as *Archaeosigillaria primaeva* and which was based upon the remarkably preserved fossil from the Hatch shale near Naples, N. Y., a splendid restoration of which is on exhibition in the State Museum at Albany. This unique specimen is usually called the Naples tree, although it was found in the upper Portage Hatch shale and is therefore well up in the upper Devonian, the name Naples being used in a geographical and not in a stratigraphical sense.

¹ White, D., N. Y. State Museum Bull. 107: 327-340, pls. 1-11, 1907.

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It was considered by White to belong to the same species that Henry D. Rogers described² in 1858 from his Cadent upper black slate at Standing Creek just east of Huntingdon, Pennsylvania as *Lepidodendron primaevum*, and which was illustrated by an extremely poor woodcut.

The horizon from which it came is usually assumed to be of Marcellus age, and in any event it is considerably older than the New York specimen. Without going into the question of the nomenclatorial history it may be pointed out that many if not all of the Devonian specimens which the older students referred to *Lepidodendron* represent more primitive types. This has been recognized by several more modern students, and Krejci in 1879 proposed the term *Protolopidodendron* for a Bohemian form which came from the Givetian stage of the Devonian, i.e. to the upper middle Devonian. Subsequently Kidston (1901) proposed the genus *Archaeosigillaria* for *Lepidodendron primaevum* Rogers and *Lepidodendron vanuxemi* Goeppert, the latter being recorded from England, and also probably occurring in Germany.³ Both genera are not precisely delimited and one or the other has been recorded from other regions, Walkom, for example, describing a *Protolopidodendron* from New South Wales. In the absence of proof of distinctness between *Archaeosigillaria* and *Protolopidodendron*, and the general unsatisfactory nature of much of the material, I prefer to use the older name of *Protolopidodendron*, which becomes the type of a distinct family, and the species under discussion becomes *Protolopidodendron primaevum* (Rogers) Berry, 1920.

The principal specimen (plate 7) is on a weathered fragment of drab shale. It shows a cortical fragment 17 centimeters long and about 6 centimeters in width. There are some indications of decay at the lower left and upper right, but I am not certain that this appearance is due to maceration before fossilization or weathering of the soft material while the surface of the piece of shale was exposed to the elements. The upper right area simulates a Knorria stage, but opposed to this are faint indications of attached leaves on both edges in the median part of the specimen, which would scarcely be consonant with a Knorria condition just above. On the other hand I have a small fragment and its counterpart from the darker unweathered shale at this outcrop which is a typical Knorria stage of this species, and which agrees exactly with the Knorria condition of the Naples tree figured by White on his plate 10, figure 1.

The larger specimen shows the fusiform, lepidodendroid scars very similar to the segment figured by White on his plate 11 which came from

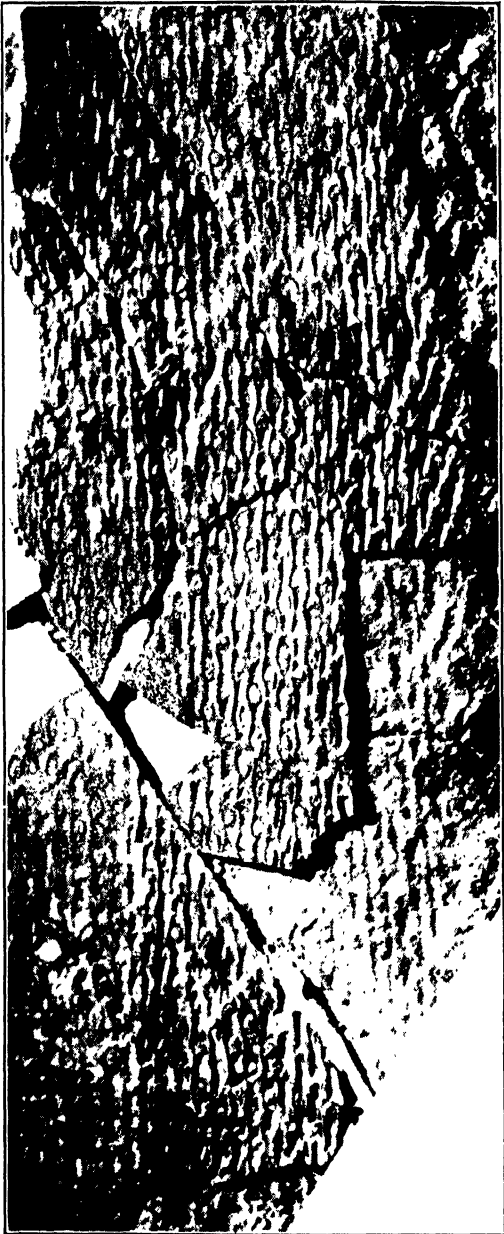
² Rogers, H. D., Geol. of Pennsylvania. 2²: 828. f. 675. 1858.

³ It is mentioned by Hume (Quart. Jour. Geol. Soc. London 88: 369. 1932) as present in southwestern Egypt, but the specific identity may well be questioned.

near the top of the Naples trunk. The Virginia specimen, however, evidently came from nearer the transitional zone of the trunk where the sigillaroid passes into the lepidodendroid form since the arrangement is not completely spiral. The preservation is not quite so good as in the New York specimen and the detailed markings of the leafscars can not be made out.

I think there can be no question but that the present material represents the same species as does the Naples tree. It is a matter of considerable interest that this, probably the largest preCarboniferous Lepidophyte, should be shown to have had such a geographic range, and it is still more interesting that it should have such a considerable stratigraphic range. Whatever the ultimate decision as to the exact horizon of the occurrence near Covington, it is obviously older than the Pennsylvania and New York occurrences, even granting that there is doubt as to whether it comes from the upper Romney or lower Jennings. If the Romney alternative proves correct it shows the presence in the middle Devonian of a primitive but rather large Lepidophyte almost as old as the middle Devonian Psilophytes (*Psilophyton*, *Rhynia*, *Hornea*, *Asteroxylon*) which have made such a stir in paleobotanical circles during the last few years. I realize, of course, that calling a fossil middle Devonian instead of upper Devonian does not alter its actual position in the stratigraphic column, but as long as men are obliged to use names and as long as geologists persist in laying so much stress on artificial time units, and correlate these units and their contained faunas and floras, just so long will the name of the unit seem more important than it really is. No other determinable plants have as yet been found associated with *Protolepidodendron primaevum* near Covington. There are a few undeterminable Lepidophyte leaves that might well belong to this same species and a parallel veined fragment that might represent a Devonian representative of the Cordaitales, but which is not certainly determinable.

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BERRY: PROTOLEPIDODENDRON

The relation of host and pathogen in *Ustilago Avenae*: a reply¹

A. ZADE AND A. ARLAND²

At the Institute of Agronomy and Plant Breeding of the University of Leipzig we have been engaged for a number of years in intensively investigating the life cycle of the loose smut of oats, *Ustilago Avenae*, in the development of methods for causing infection of oat seeds with loose smut mycelium, as well as in testing varietal immunity and fungicides. The impetus to investigate these problems was given by the important demonstration by Zade,³ published in the year 1922, that, in the case of loose smut of oats, there is a peculiar kind of blossom infection, in which the spores get into the opened flowers of neighboring plants through the agency of the wind, during the flowering period, germinate on the stigmatic branches, and form mycelium that penetrates into the glumes and gradually develops into a resting mycelium. This discovery was fully confirmed by Arland,⁴ Diehl,⁵ and Rösch⁶ in the years immediately following; and it was possible to amplify it by showing that the mycelium not infrequently attacks the outer coat of the caryopsis also, to persist here in the resting condition. Furthermore, resting mycelium was demonstrated in and on the remnants of anthers and stigmas that remained between the glumes. The spores that fell directly on the ovary during the flowering period and germinated there produced mycelial threads that appeared as if interwoven with the pubescence of the ovary. These resting mycelia, especially, however, that in the parenchyma of the outer glumes, were recognized by us as the actual infection center that must be rendered harmless by means of pickling, while previously it was assumed that it was a question of rendering the spores non-viable through pickling. We did not reject immediately as erroneous the still occasionally recurring

¹ Contribution from the Institute of Agronomy and Plant Breeding of the University of Leipzig.

² In translating this paper I have tried to make a fairly literal translation. Obviously, smoothness has been sacrificed.

"Beizen" has been rendered by "pickling," the English expression for treating seed. Again, "infizieren," which is used in the paper both in the sense of "to inoculate" and "to infect," has been translated in both ways in various places, depending on the meaning which the authors apparently had in mind.

Dr. Ernst Artschwager has been kind enough to compare the translation with the original and to make some improvements.—E. C. STAKMAN.

³ Fühling's Landwirtschaftl. Zeitg. 71: 393-406, 1922.

⁴ Bot. Arch. 7: 70-111, 1924.

⁵ Bot. Arch. 11: 146-199, 1925.

⁶ Bot. Arch. 13: 382-432, 1926.

opinion that non-germinated spores remain between the glumes and the caryopsis, and that they do not germinate until spring, after the sowing of the oat seeds, with which they germinate simultaneously; but yet it is established by our investigations, extending over many years, that spore germination in the spring can not be of appreciable importance because the viable spores germinate almost entirely at blossoming time, so that in the following spring—that is, at the time of sowing the oats—there are no, or, at most, only very occasional, non-germinated but yet viable spores within the oat seeds.⁷ Exact investigations have shown in noteworthy manner that almost all spores—indeed all, without exception—that are found between glumes and caryopsis are non-viable.

As we have been able to show conclusively, the infection of the young oat seedling proceeds from the mycelium present in the peripheral layers of the oat seed, whether it be in the parenchyma of the glumes or in other peripheral places. In the case of loose smut of oats, therefore, we are dealing, in addition to blossom infection, with a seedling infection also—a process which Zade designated “blossom and seedling infection” and which one could call “blossom infection in the sense of Zade,” in contrast to that in wheat and barley, i.e., “blossom infection in the sense of Brefeld.” This proposal is the more justifiable because Zade first called attention to this peculiar kind of blossom infection and, incidentally, discovered it at the same time for loose smut of barley, and, in agreement with Vogt,⁸ for the barley stripe disease (*Helminthosporium gramineum*).

The occurrence of this briefly described new type of floral infection has been confirmed recently in the United States also, by Gage.⁹ He obtained 67 per cent of smutted plants by inoculating oat flowers by dusting with spores. According to him the resting mycelium found in the pericarp of the caryopsis is primarily responsible for the infection of the seedlings. Furthermore, Kathleen Sampson¹⁰ demonstrated the resting mycelium in the glumes of artificially and naturally inoculated oat flowers. The importance of the resting mycelium for the overwintering of the fungus, and therefore for its life cycle, is substantiated especially by the fact contributed by Kathleen Sampson,¹¹ that the spores of *Ustilago Avenae* collected at the flowering time of oats in June, lose their viability very rapidly. According to her observation, only the completely matured spores, collected in June—that is, a considerable time after blossoming—remain viable for years.

⁷ “Haferspelzfrüchte” in original; the entire fruit is meant.

⁸ Arb. a.d. Biolog. Reichsanst. f. Land- u. Forstw. 11: 387–397, 1923.

⁹ Cornell University, Agr. Exp. Sta., Mem. 109: 3–35. 1927.

¹⁰ Ann. App. Biol. 16: 65–85, 1929.

¹¹ Ann. App. Biol. 15: 586–612. 1928.

In the following spring, according to Sampson and according to our results, an infection of the oat seedlings proceeds from the resting mycelium, while, as stated, the spores which may still be present on the caryopsis are the non-viable ones.

With the investigation of the mode of life of the fungus, however, only a part of the problem was solved. It was necessary, now, to evolve methods that made it possible to obtain, in a short time, independently of weather conditions, large quantities of certainly and uniformly infected oat seeds which are suitable for pickling experiments and for the determination of varietal immunity. The dusting of the open oat flowers with loose smut spores would be the most natural method to obtain the required infected seed material. Because of the great laboriousness, however, this method can not be used practically. As the oat flowers are open only a short time, and in cold, wet weather—at least under the climatic conditions of Germany—occasionally are not opened at all, far fewer infected kernels than are necessary for pickling and resistance investigations on a field scale can be obtained in one year, despite the activity of numerous people. The goal is reached more easily, as has been shown by investigations over a period of years, if the spores are artificially introduced between the glume and kernel and induced to germinate here. Various methods were tried before we were finally successful, after much work, in introducing the spores in a very simple manner, by suction, between glume and kernel, and to produce the mycelium here.^{12,13} The method designated as “the evacuation method,” and now more completely elaborated, makes it possible to infect almost unlimited quantities of oat seed easily with loose smut in the shortest time.

In an article that appeared in the Bulletin of the Torrey Botanical Club 57: 443–507, 1930, L. A. Kolk discussed our investigations and says, Zade and his students “have neglected to emphasize that even the early investigators of flower infection recognized that the form of the old *Ustilago Carbo* Tulasne on oats, now called *Ustilago Avenae* (Pers.) Jens., did not fit perfectly into the category either of a seedling infecting or flower infecting smut. Brefeld and Falck (1905) and Falck (1908), whose work will be reviewed later in more detail, were well aware that flower infection was possible.” (p. 444.)

In this connection it may be observed that the question raised by the authoress was not particularly mentioned in the works of Zade and his students because every one conversant with the literature on loose smut of oats must know that all the observations and conclusions pertaining to the

¹² Pflanzenbau 5: 43, 1928/29.

¹³ Bot. Arch. 29: 444–473, 1930.

old form of *Ustilago Carbo* Tulasne can be accepted only with great caution, because it was a case of a collective group which comprised the most diverse smut fungi and therefore was not infrequently the cause of confusion in the literature. Aside from this, there was no reason to go into this fully, because even the purposefully undertaken investigations of Brefeld and Falck with loose smut of oats did not lead to a solution of the problem. That Brefeld was convinced of the possibility of blossom infection is clear from his publications. Actually, Zade also called attention to this, even in his first publication.³ Furthermore, Arland discussed this fully on page 78 of his publication. The same applies to the conclusions of Falck. (See page 79 of the publication by Arland.) It is therefore incomprehensible how the authoress arrived at the assertion that Zade and his students "have overlooked especially the work of Falck in raising this question as to the place of entrance of *Ustilago Avenae* into the oat plant, . . ." (p. 445).

The view of the authoress, also, that the percentage of infection obtained by Zade and his students was in general very low when mycelium was placed between the glumes of the oat seeds or upon the epidermis of the naked kernels must be contradicted. She has overlooked the fact that since the work of Tamme, published in 1927, there are further contributions, according to which "intricate" inoculation methods are not necessary and the mycelium produced between the glumes of the oat seeds does not fail to cause heavy attack. In this connection is meant first of all the publication of Zade in "Pflanzenbau" of the year 1928/29; furthermore there are the more recent investigations of Haarring in "Bot. Archiv." Bd. 29, Heft 3/4, 1930 (appeared July 8, 1930) and in "Pflanzenbau" of the year 1930. The publications mentioned describe a very easy way which makes it possible to infect large quantities of seed with loose smut mycelium in a very short time. The method described in these publications is the "evacuation method" that has been mentioned and consists, briefly stated, in the removal by suction of the air present between glume and kernel and by the subsequent inflow of a spore suspension to permit the spores to penetrate summarily between the glumes and the kernel proper of the oat seed. In order that the spores may germinate within the glumes, oxygen is necessary, which is most easily attained by means of drying the seeds for a short time. This brings about the result that the moisture which has penetrated between glume and kernel with the spore suspension disappears and in place of it air penetrates between the glume and the kernel. Subsequent spreading of the infected seeds on moist blotting paper in a moist room suffices for the rapid development of resting mycelium. Seeds inoculated by means of the evacuation method can produce 80 to 100 per cent of diseased seedlings with proper handling. If seed inoculated in this

manner occasionally shows lower infection under conditions in the field, the inoculation method as such is not to be held responsible but rather the environmental conditions prevailing at the time of germination and infection. The authoress has therefore arrived at conclusions which, in consideration of our more recent investigations, are erroneous throughout. In addition, she did not take into consideration that inoculation methods can be developed only through protracted, fundamental investigations and much experimentation. It can not be immediately expected, therefore, that our contributions which appeared in the earliest years should furnish a complete solution of the difficult problem of the development of mycelium in a ripe oat seed.

In another connection the authoress briefly describes the new type of blossom infection. She mentions the fact that the fungus, instead of penetrating directly to the embryo, attacks principally the glumes and the epidermis of the ovary at flowering time, and later infects the young seedling that develops from such kernels. She adds, word for word: "If these claims are true, the validity of tests hitherto made for varietal resistance and susceptibility of oats to loose and covered smut (Reed, 1925a), and also tests of disinfectants used in seed treatment (Tisdale, Taylor, Leukel, and Griffiths, 1925; Leukel, 1926), where the method of dry spore inoculation has been practiced, are brought in question." (p. 444.) The authoress calls into question our results with these words, "if these claims are true," without having mentioned whether she even tested them.

Doubt must be cast on the reliability of certain investigations of Reed, who, without any consideration of the resting mycelium, induces infection by means of spores, under unnatural conditions, while we have shown clearly that the fungus, under practical conditions, brings about its effect indirectly only, by means of resting mycelium. So far as we know neither Reed nor Kolk has yet furnished proof that the testing of resistance by means of Reed's spore dusting method is irreproachable. As has been shown, resting mycelium occurs in oat seed in America also, and, if it were actually the case that there, in addition, the spores as such also remained viable between glume and kernel, to germinate into mycelia in the following spring, it would first be necessary to prove that the seedling infection caused by the spores runs parallel with that proceeding from the mycelium, and that the degree of susceptibility in the case of both types of infection would tend in the same direction. It is possible that this relationship exists, as Reed and Kolk assume; but yet, as has been mentioned, the proof has not yet been adduced.

The principal difference of opinion is in regard to the question whether it is correct to determine the effect of pickling substances on the spores or

on the resting mycelium. No one can doubt that the pickling of spores is pointless, because, as has been proved, it is not the spores that the pickling substance has to render harmless under practical conditions. A pickling substance can therefore be tested only on oat seeds containing mycelium. Spore pickling would, on condition that the seedling infection brought about by the spores parallels that caused by the mycelium, make it possible to recognize the effect of a pickling substance in case the spores would show exactly the same susceptibility to pickling as the resting mycelium. This, however, as we have abundantly proved, is not the case.

Attention may be called in this connection to still the following. Almost all of the viable spores germinate in the summer inside the oat flowers; therefore they scarcely have opportunity to overwinter in ungerminated condition. The few spores that remain undeveloped between the glume and kernel are, as has already been discussed above, in general the non-viable ones. There are still other proofs of the correctness of this conclusion, because it is significant that the spores are finely echinulate to facilitate attachment, that they are liberated at blossoming time; further, that the optimum for their germination is between 22 and 30°C. but that the optimum for the formation of mycelium lies between 18 and 26°C. Temperatures which prevail at blossoming time but not shortly after sowing, therefore are necessary for germination and mycelial formation. To attempt to consider the time consuming detour by a possible conidial formation as evidence against the presence of blossom infection, however, simply is not tenable, because, as Arland has shown, at a temperature approaching 30°C. absolutely no conidial formation occurs on the stigmas, clearly under the influence of the stigmatic secretion, but instead immediate mycelial formation occurs.

As has been said, natural conditions are not simulated if dehulled oat kernels dusted with spores are sown for the purpose of obtaining heavy attack and the seedling plants then treated in an unusual manner according to the proposal of Reed, because, practically, in the case of ordinary seed oats, hulled seeds and no naked seeds, with rare exceptions, are sown. In addition it has been shown by Haarring,¹³ that the very laborious dehulling of the seeds in Reed's method can be supplanted by simple introduction of the spores by suction, using our evacuation method. Reed germinates the dehulled oat seeds, dusted with spores, at a relatively high temperature in a substrate provided with a very small amount of water. After the development of the first leaf, he transplants the seedlings into the open. He obtains by this artificial means an attack of 100 per cent in the case of susceptible varieties, even though, or, to use the words of Haarring, "because" he does not take into consideration the natural inter-

relations between host and parasite. With justice, Haarring says, "What is the value of so high an infection figure if it is only to be attained under abnormal conditions? There develops in the young oat plants, because of the high temperature for germination and growth, a soft, weakly tissue which can not interpose any resistance to the fungus on its way to the growing point." (p. 446.) "Certainly the oat varieties to be tested need not react at all similarly to such conditions, so entirely opposite to natural ones." (p. 446.) It is clear that this method can at any rate be useful for studies of resistance, insofar as the previously mentioned parallelism is proved, but nevertheless that it is entirely unsuitable for pickling tests. It already has been mentioned that pickling substances corresponding with the natural requirements of the fungus must be tested on the peripheral resting mycelium. Preparations which had only the ability to kill spores would be of very little value to us, entirely apart from the fact that one does not observe the so-called "deep effect" in the pickling of dehulled seed, which is exactly what is necessary in the case of loose smut of oats. The favorable pickling effect of formaldehyde is doubtless attributable to its very strong "deep effect".

All in all, too much artificiality is used in Reed's method, a procedure which is directly contrary to the natural developmental processes of plant and fungus. Hence it must appear strange when Kolk says in one place "intricate and unique methods of seed inoculation have been devised" by us for the attainment of infection, while it is exactly the method of Reed, which the authoress favors, that is everything but simple. It is worthy of reflection, further, that the authoress does not mention, and probably therefore does not even know, our simple evacuation method, published in the years 1928, 1929 and 1930. While there is required, according to the results of Haarring, 32 days, of eight hours' work daily, to infect one kg. of oats with Reed's method, there is required for the infection of the same amount of oats only 4 hours with the evacuation method. One therefore definitely reaches the conclusion, that the "intricate and unique method of seed inoculation" is indeed that of Reed.

That the seed treated by Reed's method produces plants with abnormal smut attack, is shown by our investigational results, which follow. While the seed inoculated by our method always showed the tendency in infection percentages, long known in practice, for the plants developing from the inner seeds always to show a heavier attack than those developed from the outer seeds, this difference did not appear in plants developed from seed inoculated by Reed's method. Plants arising from the outer seeds behaved, according to Reed, in the same way as those from the inner seeds. In some cases the plants developed from the inner seeds even showed

a weaker attack than those from the outer seeds. According to these experimental results, therefore, one should use inner seeds for seed. At least it would be immaterial, as far as loose smut attack is concerned, according to the results obtained by Reed's method, whether outer or inner seeds are used for seed. Actually, however, it is a known fact that outer seeds must be used for seed because, as mentioned, it is established that the plants derived from them are distinctly more resistant to loose smut than the inner seed plants.

Some of our figures may be used to support this. The results were obtained from a large number of plants, and are therefore well substantiated.

	INFECTION IN PER CENT	
	OUTER SEEDS	INNER SEEDS
Seeds dehulled, caryopses dusted with spores and sown directly in the open.	16.67	16.18
Seeds dehulled, caryopses dusted with spores, the seedlings grown in boxes according to Reed's method and transplanted into the open. . . .	66.67	40.63
Seeds inoculated by our evacuation method and sown in the open. . . .	51.35	66.20

If Kolk in another connection (p. 495) reports that von Rosenstiel¹⁴ tried and compared different inoculation methods and was able to demonstrate that Reed's method was the most effective, it is to be said that in this publication the statement is indeed made that the method of Reed is marked by unconditional superiority. Kolk, however, omitted to subject to scrutiny the accompanying tables in which the actual results are given. Had she done this it would have struck her that the seed of Line 01108 inoculated with Reed's method produced an infection of only 29.6 per cent, and that of Dippes Ueberwinder one of 51.3 per cent. When, however, the seeds were inoculated by the Leipzig method and when moisture and temperature likewise were at the optimum at the stage of seedling infection, an infection of 100 per cent was attained in Line 01108 and 93.3 per cent in Dippes Ueberwinder. If seeds dehulled and dusted with spores according to Reed's method were sown directly in the open, the infection percentage was 0.0 in Line 01108, and in Dippes Ueberwinder 9.5 per cent. The seeds inoculated by the Leipzig method produced, on the other hand, 61.2 per cent infection in Line 01108, and 22.7 per cent in Dippes Ueberwinder. On careful examination of the tables it strikes one, further, that the reputed uniformity in the results obtained by von Rosenstiel by Reed's method also is not present. In this respect, also, the opposite is true. Some figures from von Rosenstiel's work will show this.

¹⁴ Phytopath. Zeits. 1: 317-360, 1930.

If, therefore, the tables are correctly interpreted, one reaches exactly the opposite conclusion to that of von Rosenstiel.

That the mycelium in the glume parenchyma plays a more important role in the subsequent seedling infection, under our ecological conditions, than that present on the outer layers of the caryopsis, appears, moreover, from experiments which we made with seed inoculated by the new evacuation method. After the spores had been introduced by suction and the formation of resting mycelium had been induced, a part of the seed was sown without further treatment. Another part of the seed was handled in this manner: smut-free caryopses, that is, kernels which had been taken

SEEDS INOCULATED BY THE LEIPZIG METHOD AND THE SEEDLINGS GROWN UNDER OPTIMUM TEMPERATURE AND MOISTURE CONDITIONS		SEEDS INOCULATED BY REED'S METHOD AND THE SEEDLINGS ALSO GROWN UNDER OPTIMUM TEMPERATURE AND MOISTURE CONDITIONS	
DIPPES UEBERWINDER	LINE 01108	DIPPES UEBERWINDER	LINE 01108
Percentages of infection			
95.7	100.0	45.6	5.5
96.7	100.0	73.7	21.6
88.6	100.0	34.6	61.9

from healthy oat seeds, were introduced between infected glumes that contained mycelium. A third lot of seeds was compounded of mycelium-free, therefore uninfected, glumes and diseased kernels which had mycelium in the pericarp. The most important thing in this connection was that the kernels should fit perfectly between the glumes in every case. For this reason provision was made for the careful sealing of the seeds¹⁶ by dipping the tips of the glumes in gum arabic. When the work was carefully done, one attained a normal growth of the plants and an irrefutable answer to the question regarding the location of the principally effective infection center. The investigations showed that by far the heaviest attack occurred when the glumes and kernel were provided with mycelium, that the attack was weaker when only the glumes contained mycelium, and weakest when only the caryopses contained it. On sowing dehulled seeds infected with mycelium, we obtained scarcely one-third the severity of attack as with hulled seeds infected with mycelium. From this it is certain that the glume mycelium represents the principal infection center under our conditions.

For the elucidation of the question as to what the situation is in hull-less oats, Rösch dusted several hundred flowers of *Avena nuda* with smut spores. Microscopic examination showed that almost all the spores germinated just as in the case of hulled oats. Rösch, however, calls attention in this connection to still another kind of infection, which may have a certain significance, especially in the case of hull-less oats. He writes: "In general, most of the smut spores are liberated at the time the oats are harvested.

¹⁶ Spelzfrüchte in original.

Often, however, the smutted panicles of individual belated culms, because of too late development, remain in the leaf sheaths. On threshing, then, these culms are broken up, the spores fly about in the threshing machine, and can attach themselves to the naked oat seeds." (p. 385.) Since, according to the previously mentioned demonstration of Sampson, only the completely mature spores, that is, those collected in July, a considerable time after blossoming, retain their viability for years, it is by all means necessary to reckon with this mode of infection in the case of hull-less oats. That this, however, is of very slight significance in the case of hulled oats, as hulled oat seeds dusted externally with spores produce virtually no infected plants, is sufficiently well known. The explanation for this is given by Zade³: "The seedling develops directly from the dehulled seed and, as soon as it has broken through the seed coats, the infection, that is, the penetration of the fungus mycelium into the plumule of the leaf, can proceed immediately. This process is different in the case of seed enveloped in the glumes. In this case the seedling can be infected only after it has pushed out through the glumes, that is, when it has traversed approximately 1 cm. longitudinally between glume and kernel, because normally the plumule of oats grows within the glume envelope up to the glume tip, there first to reach the outside. An oat seed, therefore, can be considered to have germinated, in contrast to rye and wheat, only when the plumule becomes visible, not as soon as it has broken through the pericarp of the caryopsis. An infection by means of the spores possibly adhering to the outside of the glume envelopes would therefore be possible only after the time when the plumule has left the tips of the glumes, and in this stage of growth it is no longer so tender and so susceptible as at the time of the breaking forth from the envelope of the kernel. In nature several days usually elapse, at low temperature under certain conditions weeks after sowing, before the plumule which has proceeded from the caryopsis leaves the glume tips behind and is accessible to infection by the smut fungus. Furthermore, it is to be noted that the spores on the outside of the hulled seed, insofar as they do not happen to be on the tip, are scarcely able to produce fungus threads long enough to reach and attack the seedling. In other words, the spores which may germinate can reach their goal only in rare cases." (p. 399.)

The view of Kolk that the presence of mycelium in the glumes is not to be considered "an actual invasion of the host" is not correct. It is far more a case of actual infection, because the mycelium penetrates into the fresh green plant tissue and ramifies it. It is not comprehensible why the presence of mycelium in the growing point of the embryo or in other parts except the protecting glumes is necessary, for justification of the concept

of infection. The infected floral envelope belongs to the flower just as much as does the embryo.

That *Ustilago Avenae*, after previous blossom infection, penetrates into the host plant by means of seedling infection, Zade and his students have never doubted, but rather always supported. In particular the penetration of the fungus into the young oat seedling, that is, seedling infection, is described accurately on the basis of detailed investigations and, in addition, illustrated by figures in the works of Rösch⁶ and Haarring.¹³ Naturally, seedling infection is not only present when the mycelial threads growing from the recently germinated spores penetrate the seedling, but also when the infection proceeds from the peripheral resting mycelium.

To go into detail with respect to further points in the work of Kolk would probably be superfluous in this connection. We reserve an amplification of our reply for another place.

The production of vestigial and sterile sex-organs through sex-reversal and neutral sexual states¹

JOHN H. SCHAFFNER

(WITH PLATE 8)

The vascular plants fall naturally into two fundamental groups in respect to the sexual condition of their sporophytes. In the lower level, the sporophytes are normally entirely neutral showing no sex dimorphism at any stage of their life, while in the higher level, the sporophytes always develop sexual states and show sex dimorphism before the completion of their ontogeny. In any consideration of the sexual conditions of the vascular plants, the recognition of the nature of the evolution of the time of sex determination in the life cycle becomes of paramount importance. Apparently the bisexual state is present in all sporophyte individuals of the living heterosporous pteridophytes and is plainly also the original condition for all angiosperms, the monoecious or dioecious conditions being secondary in the evolutionary sequence. In the fossil gymnosperms there are examples of the bisporangiate or bisexual condition and in a few living species the presence of vestigial structures of the opposite set of sporophylls in the flowers indicates an original bisporangiate condition. In the living cycads and conifers, however, no vestigial structures of the opposite sporophylls appear, and we can assume, as a reasonable hypothesis, that these plants had monoecious branches before flowers had evolved, namely before a determinate condition of the reproductive branch was attained. Thus there would be no functional gradients developed in a given determinate branch which might cause the production of both male and female states and thus bring into play hereditary factors for male and female characters. From the monoecious condition, either directly or through a series of degrees of monoeciousness, the final dioecious condition then evolved in various gymnosperm lines and apparently, since the original individual flowers were never dimorphic in respect to sex, the dioecious species also never show vestiges of the opposite sex organs.

In the angiosperms, however, the primitive, or original condition of the flower is bisexual and from this condition monoeciousness in all degrees of promptness of development and degrees of intensity and also dioeciousness in various degrees of intensity of the one or the other sexual state of the individual evolved. The nature of the sexual phenomena exhibited by the taxonomic system of the angiosperms indicates plainly that sexuality is a fundamental potentiality and that the various sexual states and con-

¹ Papers from the department of botany, The Ohio State University, No. 309. Read at the Sixth International Congress of Genetics, Ithaca, New York.

ditions, ranging from normal femaleness through neutrality to normal maleness, result from physiological conditions or gradients in individual cells or cell lineages. These implications are fully confirmed by experimental results, which up to the present time have been occupied largely with the production of sex-reversal and control in both monoecious and dioecious plants. Little if anything at all has been done in attempted control of sexual expression in bisporangiate flowers, although one occasionally sees complete transformation of one set of sporophylls to the other in such bisporangiate flowers.

In the original flower type of the angiosperms, the floral axis passes from a neutral state to the secondary male state and then by a prompt reversal to the secondary female state. In various primitive types of such flowers, however, the reversal of the growing flower bud from the male to the female condition is rather slow so that a considerable neutral development takes place in the transition which may manifest itself in several ways. Thus in species of *Michelia*, *Geum*, *Nelumbo*, etc. there is a prominent development of an internode separating the stamens below from the carpels above. In *Michelia* the internodal development between the androecium and gynoecium is sometimes as much as a centimeter or even more. This neutral condition is also indicated by the long stipitate condition of the gynoecium found in the flowers of various species of *Baptisia*, *Meibomia*, *Subularia*, *Lunaria*, *Cleome*, *Cristatella*, etc.

In *Aquilegia canadensis* L. and other species the neutral zone between the stamens and carpels develops a number of distinctive bracts which are typical neutral organs unlike either the stamens or carpels. Another rather primitive type of flower which shows prominent neutral structures between the gynoecium and androecium is *Calycanthus floridus* L. The entire receptacle is expanded into a cup and the neutral transition ring of tissue between the central carpellate region and the outer staminate rim is occupied by prominent, short, sterile bracts which are on the one hand much like stamens but without microsporangia and on the other like imperfect carpels. The neutral transition thus bears carpellobes next to the normal carpels and staminodes next to the normal stamens while the central part contains bracts intermediate in nature. The staminodes next to the normal stamens sometimes bear minute, imperfect microsporangia. In general, the decided determinateness of the floral axis of the higher types of flowers should not permit of such intermediate structures and apparently neither internodes nor neutral bracts appear on the transition zone of the higher bisporangiate flower types, because in these the general determination of the system develops much more rapidly than in the lower.

The evolution of monoeciousness from the bisporangiate flower con-

dition is accomplished in various ways, the most interesting for the present discussion being the type in which the inflorescence axis produces first carpellate flowers and later, through sex-reversal staminate flowers or with a progression from the neutral vegetative condition in the opposite sequence, first staminate flowers and then carpellate. The evolution of this type of monoeciousness often appears to be in an orthogenetic sequence, producing an orthogenetic series of inflorescences. In the Alismataceae, *Echinodorus cordifolius* (L.) Griseb. has bisporangiate flowers, *Lophotocarpus calycinus* (Engelm.) Sm. has bisporangiate flowers below and staminate flowers above, while the typically monoecious *Sagittaria latifolia* Willd. has carpellate flowers below and staminate ones above. *Sagittaria* is a primitive type of monocotyl and the flowers are in general in a very primitive condition. Thus when the sex-reversal from femaleness to maleness takes place in the inflorescence axis, a neutral transition zone is necessarily produced and since it is entirely due to developing physiological gradients it frequently happens just at the level where incipient flower buds are developing. Thus these buds begin their growth as neutral systems just as they do in *Echinodorus* or as the flowers of *Sagittaria* did before monoeciousness had evolved. The result is frequently the development of one or more bisporangiate flowers on the transition zone.

The same evolutionary sequence is shown in the lower aroids and other groups. *Acorus Calamus* L., for example, has its spadix covered with bisporangiate flowers; in *Orontium aquaticum* L. there are often a few staminate flowers at the very tip, the rest being bisporangiate; in *Calla palustris* L. the flowers of the upper part of the spadix are staminate; while in species like *Zantedeschia aethiopica* (L.) Spring. and *Peltandra virginica* (L.) Kunth. the normal monoecious condition has been attained, the flowers at the lower end of the spadix being carpellate and those above being staminate. In some of the higher types of aroids, like species of *Helicodiceros* and *Helicophyllum*, which have more complex hereditary systems, the neutral transition zone of the inflorescence axis develops peculiar and characteristic structures, internodes, and outgrowths which are neither stamens nor carpels. The reactions correspond to those that occur in the flowers of *Michelia* and *Aquilegia*.

Zizania aquatica L. and *Ricinus communis* L. are examples of monoecious inflorescences which have the staminate flowers below and the carpellate ones above, and in both cases, as in *Sagittaria latifolia*, bisporangiate flowers are commonly produced on the neutral transition zone, especially in *Zizania*.

In the monoecious *Typha latifolia* L., the carpellate flowers are below and the staminate above. Since the two halves or even small segments of

the inflorescence bud may be in different physiological states, a chimera-like effect is often produced in the distribution of areas or bands of carpellate and staminate tissues. On the transition line between the two conditions there may be a neutral zone of greater or less extent, and since the spiral position of the flowers on the inflorescence is not at all dependent on any special sexual state, but is determined by the fundamental hereditary potentialities, the flowers are often situated exactly on the middle or on the sides of these neutral bands of tissue. The result is that frequently these flowers are decided sex mosaics. Sometimes a stigma may be nearly normal on the one side and develop a microsporangium on the other. Another extreme condition which is sometimes produced is the development of pollen-grains inside of the stigma.

Arisaema triphyllum (L.) Torr. is a peculiar type of dioecious plant in that its sexual condition is dependent very largely on its environment. Its functional states are, therefore, easily controlled in such a way that the inflorescence is thrown into a sex mosaic with spots or bands of male and female tissue. Thus, as in *Typha*, a zone of neutral tissue may develop where the two tissues of opposite sexual states come together, although the male and female areas may also be closely contiguous. In the first case, neutral, horn-like structures may develop where otherwise there would be a normal staminate or carpellate flower. If there is no intervening neutral zone of any appreciable width, then the flowers which appear on the transition line will themselves be sex mosaics, sometimes having one or more pollen-sacs on the side of the ovulary toward the male tissue, or even having a stigmatic structure only on the side toward the female tissue and one or more pollen-sacs on the side toward the male tissue.

Bisporangiate flowers or flowers representing extreme sex-mosaics have also been observed to occur regularly on abnormal, monoecious *Salix amygdaloides* Anders. These willows were evidently mutants from the normal dioecious form. They regularly produce catkins which have normal staminate flowers below and normal carpellate flowers above. The transition zone is quite broad indicating a slow reversal of the catkin axis from male to female during its ontogeny. Some of the sex mosaics were observed to have microsporangia imbedded in the walls of the ovulary, others approached more nearly the bisporangiate flower type, while some were normal bisporangiate flowers. These willow trees have existed for many years on a farm in Kansas and their sex reactions are in complete agreement with what takes place in similar, normal, monoecious types or with the reactions following experimental sex reversals in both monoecious and dioecious species.

One of the very striking phenomena to be observed in the angiosperms

is the presence and distribution of vestiges of the opposite type of sex organs in the monosporangiate flowers of both monoecious and dioecious species. All monosporangiate angiospermous flowers have plainly come from bisporangiate ancestral species, as stated above, through the progressive evolution of the time of sex determination in the sporophyte. This progression is a backward movement through the ontogeny and reaches its determinate limit when the sexual state is determined in the fertilized egg itself, resulting in a dioecious condition, where the individuals of both the gametophyte and sporophyte are normally unisexual. The development of the male or female state in a tissue or individual varies both in intensity and promptness and these conditions determine the presence or absence of vestigial organs or their degree of perfection in comparison with the normal sporophyll condition. The character and distribution is in general the same in monoecious and dioecious flowers. Cases in which vestiges are present in one flower and not in the other, whether in monoecious or dioecious species are to be regarded as sexual dimorphisms or sex-limited characters the same as dimorphisms in the vegetative parts.

There are four general types of distribution of the vestigial sporophylls in monosporangiate flowers: 1, both carpellate and staminate flowers with vestiges of the opposite sporophylls; 2, carpellate flowers with vestiges, staminate flowers without vestiges; 3, carpellate flowers without vestiges, staminate flowers with vestiges; 4, both carpellate and staminate flowers without vestiges. Below are given examples of monoecious and dioecious species for each type.

1. Both carpellate and staminate flowers with vestiges. **MONOECIOUS:** *Rumex altissimus* Wood, *Cucumis sativus* L., *Silphium integrifolium* Mx., *Musa sapientum* L., *Eriocaulon compressus* Lam., *Cocos nucifera* L., *Zizania aquatica* L., *Tripsacum dactyloides* L., *Coix Lachryma-Jobi* L. **DIOECIOUS:** *Phoenix dactylifera* L., *Asparagus officinalis* L., *Bulbilis dactyloides* (Nutt.) Raf., *Chamaelirium luteum* (L.) Gr., *Aruncus Aruncus* (L.) Karst., *Sassafras Sassafras* (L.) Karst., *Ailanthus glandulosa* Desf., *Diospyros virginiana* L., *Gymnocladus dioica* (L.) Koch, *Acer platanoides* L., *Lychnis alba* Mill.

2. Carpellate flowers with vestiges, staminate flowers without vestiges. **MONOECIOUS:** *Zantedeschia aethiopica* (L.) Spreng., *Peltandra virginica* (L.) Kunth, *Zea Mays* L. (some varieties). **DIOECIOUS:** *Menispermum canadense* L., *Napaea dioica* L., *Smilax hispida* Muhl., *Vallisneria spiralis* L.

3. Carpellate flowers without vestiges, staminate flowers with vestiges. **MONOECIOUS:** *Buxus sempervirens* L., *Ambrosia trifida* L., *Amaranthus*

retroflexus L., *Quercus alba* L. DIOECIOUS: *Phoradendron flavescens* (Pursh) Nutt., *Antennaria plantaginifolia* (L.) Rich., *Carica Papaya* L., *Rumex Acetosella* L., *Morus rubra* L.

4. Both carpellate and staminate flowers without vestiges. MONOE-CIOUS: *Ricinus communis* L., *Alnus Alnus* (L.) Britt., *Hicoria ovata* (Mill.) Britt., *Sicyos angulata* L., *Typha latifolia* L., *Sparganium eurycarpum* Engelm., *Alocasia odora* C. Koch, *Naias flexilis* (Willd.) R. & S., *Zannichellia palustris* L. DIOECIOUS: *Populus deltoides* Marsh., *Salix purpurea* L., *Fraxinus americana* L., *Acer Negundo* L., *Cannabis sativa* L., *Arisaema triphyllum* (L.) Torr., *Humulus japonicus* Sieb. & Zucc., *Thalictrum dioicum* L.

The true nature of sexuality and the vestigial structures which appear in monosporangiate and reversed flowers having been indicated by the taxonomic series and by direct experiment, a practical application could be made in the production of neutral, vestigial sporophylls. Indian corn (*Zea Mays* L.), which is a monoecious plant of the extreme type, just one step from the dioecious condition, in which the lower part of the main stem is neutral, the middle branches female, and the top of the main stem male in normal sex expression, seemed a very favorable species to demonstrate experimental control of the neutral state, since there is a definite gradient of physiological states in the ontogenetic development from the juvenile to the mature condition. The main stem continues in the neutral state until the reproductive phase is approached when the physiological gradient develops toward maleness. The secondary male state is finally established and when the inflorescence is developed, it is purely male in character expression, no external vestige of the gynoeceum appearing in the flowers. This shows that at the time of flower development the secondary male state is fully and intensely established. In most varieties, the lateral female inflorescence shows minute vestiges of stamens around the ovulary. This indicates that the secondary female state was not developed to the extreme degree at the time when the sporophylls began to be determined. Both the side branches with their ears and the terminal stalk with its tassel are definitely determinate systems under ordinary environmental conditions of growth, the reproductive reaction initiating determinateness or stopping of growth and bringing on death at the end of the differentiation process.

Since the terminal bud can easily be thrown over to femaleness during its growth, even at an early period by a properly controlled environment, in which a short daylight period is a very essential factor, it follows that the terminal bud of the main stem can be brought to the neutral point just at the time when the reproductive process is beginning to take place. But

the reproductive process in the flower requires the presence of the secondary male state or physiological activity in order to bring about stamen development, or the secondary female state or female physiological activity in order to bring about carpel development. In the normal gradient toward the tassel, maleness has been attained at this point and normal staminate flowers develop. If the system has been somewhat lowered in physiological activity the tassel may develop as a sex mosaic and produce carpellate and bisporangiate flowers as well as staminate ones. Or if the system has been lowered so that the bud is in the secondary female state at the beginning of flower production, normal carpellate flowers only will be expressed as in the lateral inflorescence. Now if the bud is at the zero point in relation to the sex balance nothing can be in activity, since there is neither a secondary female state nor a secondary male state in the cells there can be no secondary sex factors thrown into activity and so there are no staminate nor carpellate flowers produced. On the other hand, the terminal bud can not continue vegetative growth because of the development of extreme determinateness in the entire system. Thus the whole tassel is matured as a minute vestige, often not more than one or two centimeters long on a very slender peduncle. This vestige is the neuter expression of the sexual reproductive organs of the Indian corn. Although the experimental method depends on a very accurately timed physiological balance in relation to maturity, from 20-40 per cent of neutral tassels can easily be produced in a given population.

Since the floral development in Indian corn begins somewhere near the middle of the inflorescence and proceeds from there toward the base and apex at the same time, it follows that if the system has advanced toward the female condition so that the reversal will take place before the first flowers are determined, then the floral development will proceed with the secondary female state to the base of the inflorescence axis, and a fair-sized ear or female inflorescence will result. But the outer end of the inflorescence axis will have only a neuter vestigial tip since the determinate ontogenetic gradient will prevent a progression to the female state or to a renewed vegetative growth. The little terminal ear always has a sterile or neutral tip just as is usually the case in a side inflorescence or normal lateral ear.

If the ecological conditions are so controlled that the physiological state has not attained to femaleness when the first central flowers of the inflorescence develop but is nevertheless soon to pass over to that condition, then the secondary male state may be developed at this point and a zone of staminate flowers will be produced which will soon pass over to the neutral condition both above and below. If now the ecological factors have

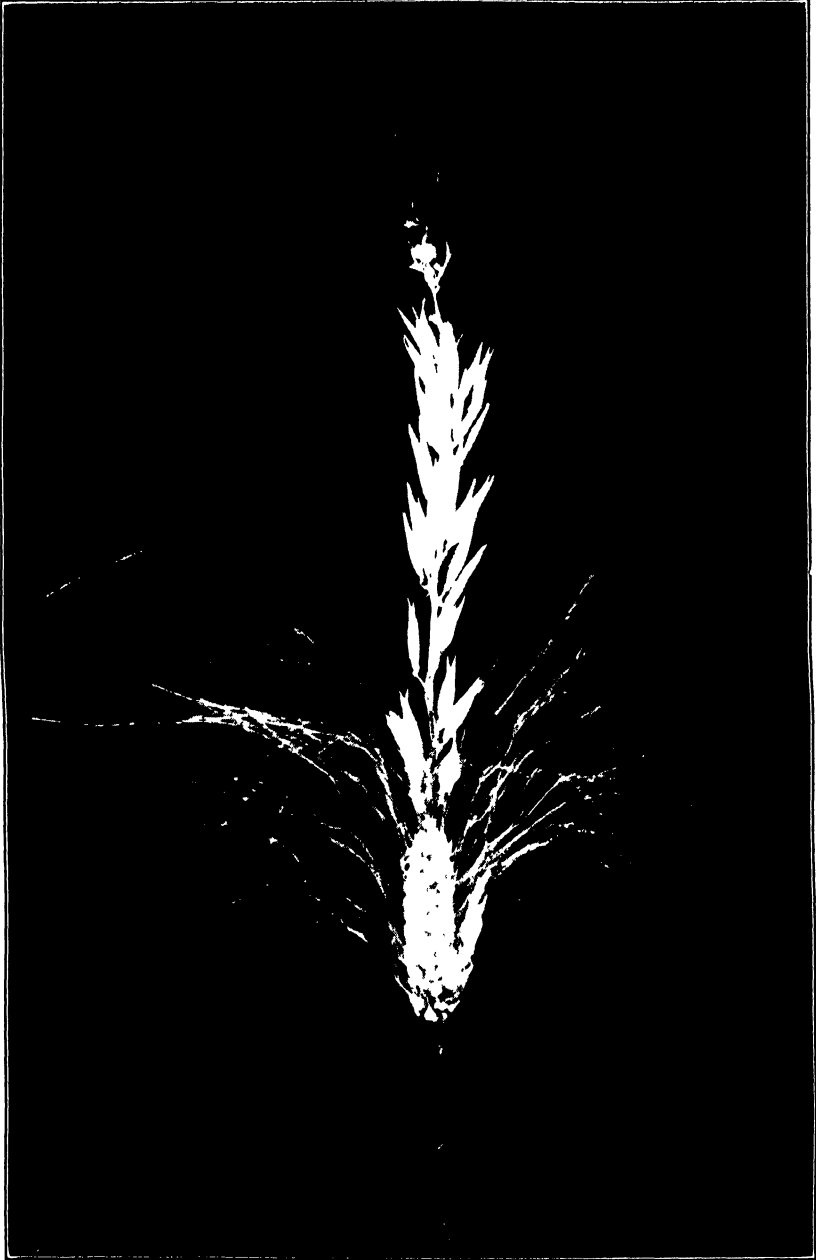
been so controlled by increasing the length of daily illumination at the proper time in the ontogeny there will promptly be developed a greater physiological vigor and this will delay the determination at the tip of the axis enough to allow a female state to arise, then the axis of the inflorescence will, after passing through the upper and lower neutral conditions produce female structures at the outer end as well as at the lower. The inflorescence which results will then consist of five definite zones, namely a central zone of staminate spikelets and flowers with a neutral transition zone of vestigial spikelets on each side of this with female expression resulting in little ears at the two extremes (plate 8). Thus instead of the usual branched staminate tassel we have the remarkable result of a sex mosaic consisting of five zones, (1) a basal female zone with normal fruit development, (2) a neutral vestigial zone, (3) a zone of normal staminate flowers, (4) a second neutral zone, followed by (5) a second female zone with normal fruit development at the outer tip. On account of the complexity of the physiological gradients one can only occasionally produce this result, although it is not difficult to bring out female expression at the ends of the main axis or branches of the inflorescence. These expression phenomena are all clearly consistent with what we know of the ontogenetic and physiological gradients and are consistently interpreted by the physiological theory of sexuality. Any attempt to seek an explanation of sexuality and sex in terms of a balance of genes instead of a balance of physiological states would be beside the mark, since in all of these processes the balance of genes apparently remains exactly the same. The ordinary vegetative karyokineses are continuing the original diploid complement of chromosomes and balance of genes just as definitely as we know they do when varieties of fruit are propagated indefinitely by means of grafting and stem cuttings.

A multitude of such phenomena which confront the taxonomist shows that the genetic hypotheses of sex and sex-determination are entirely untenable and have no correspondence with the actual conditions in which sex is manifested in the plant kingdom.

An investigation of the nature and causes of neutral states, sterility and imperfect sex expressions must lead to developments of far-reaching importance both in general biology and in the biology of human sex conditions. The bees and various other insects have evolved hereditary constitutions through which they instinctively produce males, females and partial neuters at will. Through the reactions of the workers in producing cells of the proper size and the subsequent feeding of the larvae on the one hand and on the other probably through the instinctive nervous reactions of the queen, the sexes of the normal colony are very decidedly controlled.

Partial neuter conditions and partial sex-reversals are common in humans and it is of the greatest importance to the welfare of society that the exact causes of neutrality, sex-reversal, and sterility of both males and females be discovered and proper treatments be developed to overcome barrenness and undesirable neutral and reversed mental reactions. It frequently happens that those who have the highest mental endowment and otherwise a normal physical condition cannot perpetuate their desirable hereditary lines. The proper study of neutrality in plants may prove as enlightening for the problem of human sterility as the mendelian study of plant heredity proved to be for the problem of animal heredity.

COLUMBUS, OHIO.



SCHAFFNER: SEX IN INDIAN CORN

Studies of South American Plants. III.

New Ericaceae and Vacciniaceae

ALBERT C. SMITH

In the accompanying paper specimens from several large herbaria are cited. These institutions are indicated by the following abbreviations: Botanisches Museum, Berlin-Dahlem (B); British Museum (BM); Herbarium Boissier, University of Geneva (Bo); Conservatoire Botanique, Geneva (C); Royal Botanic Gardens, Kew (K); U. S. National Museum (N); Muséum d'Histoire Naturelle, Paris (P); New York Botanical Garden (Y).

ERICACEAE

Gaultheria Tatei sp. nov. Frutex parvus compactus; ramulis subteretibus fuscis, juventute puberulis ac etiam parce glanduloso-setosis, mox glabrescentibus; petiolis subrugosis nigrescentibus decidue setosis 2–3 mm. longis; laminis coriaceis ovato-oblongis, 2–3 cm. longis, 1–1.5 cm. latis, basi rotundatis vel obtusis, apice subacutis et nigro-callosio-mucronatis, margine leviter incrassatis et crenulato-serratis (dentibus 10–15 per centimetrum), utrinque subglabris (juventute parce setosis) et nigro-punctatis, pinnatinerviis, costa supra leviter impressa subtus prominente, nervis secundariis 3- vel 4-jugis brevibus arcuato-adscendentibus, supra subplanis subtus elevatis, venulis subtus conspicue reticulatis; inflorescentia copiosa prope apices ramulorum axillari, racemosa 8–12-flora; rhachide 2–3 cm. longa velut ramulis juvenilibus puberula et glanduloso-setosa, basi bracteata; pedicellis gracilibus velut rhachide pubescentibus 7–9 mm. longis, bracteis coriaceis lanceolato-obovatis 4–5 mm. longis subtentis (bracteis margine puberulis et glanduloso-ciliatis), bracteolis minoribus prope basin bibracteolatis; florum partibus exterioribus ubique parce albo-puberulis ac etiam parce glanduloso-setosis (pilis 0.5 mm. longis); calycis lobis elongato-deltaideis sub anthesi circiter 4 mm. longis et 2 mm. latis; corolla tenuiter carnosa cylindrico-urceolata, maturitate 6–7 mm. longa et 3–4 mm. diametro, lobis 5 oblongis obtusis circiter 1.5 mm. longis; staminibus 10, 4–4.7 mm. longis; filamentis stramineis ligulatis gracilibus 3.5–3.8 mm. longis, pilos delicatulos ad 0.5 mm. longos gerentibus; antheris aristis brevibus inclusis circiter 1.5 mm. longis; ovario depresso-globoso sub anthesi circiter 2 mm. diametro albo-puberulo; stylo carnoso 3–3.5 mm. longo, stigmate truncato.

Type, *G. H. H. Tate 217*, collected in 1925 on sub-páramo on Cerro de Turumiquire, State of Sucre, Venezuela, alt. 3000 meters, and deposited in the U. S. National Herbarium (no. 1,230,901). It is a species allied to *G. reticulata* H.B.K., which it resembles very closely in foliage, but from which it differs by having the venation less obvious on the upper leaf surface. In floral aspect, the new species has the calyces and corollas pubescent

rather than glabrous, the calyx lobes more acuminate, and the bractlets of the pedicels longer.

Gaultheria megalodonta sp. nov. Frutex; ramulis elongatis (dependentibus?) subteretibus nigrescentibus glabris; petiolis subrugosis glabris 1–2 mm. longis; laminis coriaceis glabris supra nitidis late ovatis vel suborbicularibus, 15–20 mm. longis et latis, basi truncatis vel subcordatis, apice calloso-apiculatis, margine valde serratis (dentibus 6 vel 7 per centimetrum), pinnatinerviis, nervis secundariis 2- vel 3-jugis, e costa prope basin orientibus, arcuato-adscendentibus, cum costa utrinque elevatis, venulis paucis reticulatis utrinque elevatis; inflorescentia axillari apices ramulorum versus congesta, racemosa, quam foliis duplo vel triplo longiore, 12–20-flora; rhachide subtereti recta 3–5 cm. longa, minute pallide puberula ac etiam pilis ferrugineis circiter 1 mm. longis setosa; pedicellis gracilibus 4–8 mm. longis, velut rhachide pubescentibus, bracteis deciduis coriaceis parce fimbriatis oblongis 5–7 mm. longis subtentis, prope basin bibracteolatis, bracteolis oblongo-subspatulatis circiter 3 mm. longis fimbriatis; florum partibus exterioribus juventute ubique minute pallide puberulis, mox glabrescentibus, 5 (raro 6)-meris; calycis lobis deltoideo-ovatis acutis sub anthesi circiter 3 mm. longis et 1.5 mm. latis; corolla cylindrico-campanulata, maturitate 6–7 mm. longa et 3–4 mm. diametro, lobis deltoideis obtusis circiter 1 mm. longis et latis; staminibus circiter 3.5 mm. longis; filamentis pallide castaneis subglabris, 2.5–3 mm. longis, prope basin circiter 0.5 mm. latis, superne contractis; antheris leviter granulatis, aristis brevibus inclusis 1–1.3 mm. longis, per poros ovaes subapicales dehiscentibus; ovario subgloboso, sub anthesi circiter 2 mm. diametro, minute molliter piloso; stylo 3–3.5 mm. longo, stigmate subcapitato.

Type, *Pearce*, collected in Ecuador, alt. about 3700 meters, and deposited in the herbarium of the Royal Botanic Gardens, Kew. It is a very distinctive species by virtue of its densely aggregated racemes and its suborbicular coarsely serrate leaves. Probably it is related to *G. reticulata* HBK., from which it differs by having the leaves proportionately broader, often subcordate at base, more obviously serrate, the venation less closely reticulate, and the pubescence of rachis and pedicels more pronounced.

GAULTHERIA INSIPIDA Benth. and its allies: *G. insipida* Benth. and four allied species form a very natural group in the northern Andes. The species are characterized by the straight subappressed strigose hairs of the branchlets and by the bullate leaves with conspicuous secondary veins. The five species may be distinguished among themselves thus:

Calyx glabrous.

Leaves not arachnoid-lanate.

Leaves rounded at base, long-setose at margin; calyx lobes acuminate *G. insipida*

Leaves subacute at base, short-setose at margin; calyx lobes acute... *G. tolimensis*

Leaves arachnoid-lanate beneath..... *G. arachnoidea*

Calyx densely strigose.

Leaves nearly plane or slightly recurved at margin, more than 10 mm. broad *G. strigosa*
 Leaves tightly revolute at margin, 5-8 mm. broad..... *G. revoluta*

GAULTHERIA INSIPIDA Benth. Pl. Hartw. 225. 1846. *Gaultheria petraea* Wedd. Chlor. And. 2: 174. 1860. The two type specimens here concerned show no essential differences, the species being very consistent throughout its range. It grows at altitudes from 2400-3600 meters, and is represented by:

COLOMBIA: Minas, *Lehmann B. T. 1059* (Y). Tolima: Mt. Tolima, *Tracey 232* (K). Quindio Region, *Dawe 734* (K, Y). El Valle: Alto San Antonio, near Cali, *André 2644* (K). El Cauca: San Antonio, *Pennell & Killip 7297* (K, Y), *7298* (Y), *7431* (Y), *Pennell 7567* (Y). Cuatro Esquinas, *Pennell & Killip 6331* (Y). Río Palace, near Popayan, *Lehmann B. T. 640* (K, Y). Río Micay, *Lehmann B. T. 641* (C). Nariño: Pasto, *Triana 2642* (B, C, K). Páramo de Guapuscal, near Pasto, *André 3144* (K, Y).

ECUADOR: *Hall 3* (K), *4* (K). *Sodiño 93/3* (B). Pichincha: *Jameson* (K), *29* (Y), *75* (BM, C, P, type of *G. petraea*¹). Between Quito and Machachi, *Hartweg 1229* (C, K, type). Mt. Pichincha, *Jameson 17* (K), *276* (K), *309* (BM, C, K). Between Malchinguí and Pomasquí, *Hitchcock 20878* (Y). Tunguragua: Mt. Tunguragua, *Spruce 5107* (BM, C, K). Azuay: Cuenca, *Warszewicz* (B).

GAULTHERIA TOLIMENSIS Wedd. Chlor. And. 2: 173. 1860. The differences between this species and the preceding are not strongly marked. It is found at elevations of 3400-3900 meters, and is represented by:

COLOMBIA: Tolima: *Goudot 2* (K, P). Mt. Tolima, *Linden 919* (C, P, type). Cerro de perro, near Ibagué, *Goudot 1* (P). Quindio region, *Linden 1119* (C, P). Caldas: Cerro Tatama, *Pennell 10569* (Y).

Gaultheria arachnoidea sp. nov. Frutex compactus; ramulis teretibus brevibus, juventute pilis crassis ferrugineis 1.5-2 mm. longis dense strigosis ac etiam parce albo-arachnoideo-lanatis, demum glabrescentibus; petiolis circiter 2 mm. longis velut ramulis pubescentibus; laminis coriaceis ovato-oblongis, 18-30 mm. longis, 7-11 mm. latis, basi acutis, apice breviter acuminate, margine subintegris et valde revolutis, supra ferrugineo-strigosis mox glabrescentibus, subtus pilis 1.5-2 mm. longis persistenter strigosis ac etiam pilis minutis laxis dense et arcte albo-arachnoideo-lanatis, pinnatinerviis, costa supra impressa subtus prominentissima, nervis secundariis 3- vel 4-jugis patulis, supra planis, subtus elevatis indumento saepe occultis, venulis reticulatis; inflorescentia axillari breviter racemosa 5-9-flora; rhachide gracili 7-12 mm. longa, pilis ferrugineis patulis ad 1 mm. longis dense pilosa; pedicellis gracilibus 3-5 mm. longis, pilos circiter 0.5 mm. longos gerentibus, bracteis ovatis subglabris breviter fimbriatis circiter 3 mm. longis subtentis, prope basin bibracteolatis, bracteolis 2 mm. longis; calyce subcoriaceo glabro, lobis 5 deltoideis acutis, sub anthesi circiter 2.5 mm. longis et 2 mm. latis; corolla

¹ Although the type of *G. petraea* is cited as *Jameson 196*, that number is not found at Paris. *Jameson 75* bears notes which indicate that Weddell's species was based upon it.

tenuiter carnosae glabrae obovatae, maturitate circiter 5 mm. longae et 4 mm. diametro, superne contractae, lobis 5 oblongis obtusis circiter 1 mm. longis et latis; staminibus 10 circiter 3.5 mm. longis; filamentis ligulatis s. ramineis parce puberulis circiter 2.5 mm. longis; antheris oblongis, aristis brevibus inclusis 1.3–1.5 mm. longis, per poros subapicales dehiscentibus; ovario subgloboso sub anthesi circiter 2 mm. diametro, minute molliter piloso; stylo crasso circiter 3 mm. longo, stigmate subcapitato.

Type, *Jameson 499*, collected on Volcano of Pasto, Department of Nariño, Colombia, alt. about 3700 meters, and deposited in the herbarium of the Royal Botanic Gardens, Kew. Duplicates at BM, C, Y. It is a species which differs from its allies *G. insipida* Benth. and *G. tolimensis* Wedd. by the unique pale arachnoid indumentum of young branchlets and lower leaf surfaces, and also by having the leaves smaller and more closely revolute.

GAULTHERIA STRIGOSA Benth. Pl. Hartw. 221. 1846.

COLOMBIA: *Bonpland* (P). *Lehmann B. T. 1059* (K). Cundinamarca: Páramo de San Fortunato, near Bogotá, *Hartweg 1211* (B, BM, C, K, type, P). Between Sibaté and San Fortunato, *Triana 2640* (P). Near Sibaté, *Linden 813* (BM, C, P). Fusagasuga, *Triana 4323/5* (B). Tolima: Quindío region, *Goudot* (P). Antioquia: Alto San José, *Kalbreyer 1883* (B, K). Caldas: Cerro Tatama, *Pennell 10523* (Y).

Gaultheria revoluta sp. nov. Frutex parvus compactus; ramulis subteretibus rectis rigidis, juventute pilis ferrugineis aristatis 1–1.5 mm. longis dense strigosis, demum glabrescentibus et cinereis; petiolis subrugosis subteretibus decidue strigosis circiter 2 mm. longis; laminis coriaceis ovato-oblongis, 15–23 mm. longis, 5–8 mm. latis, basi ac apice acutis, margine integris vel minute crenulatis et valde revolutis, utrinque pilis deciduis 1 mm. longis ferrugineis strigosis (pilis subtus costa persistentibus), pinnatinerviis, costa supra impressa subtus prominentissima, nervis secundariis 3-vel 4-jugis brevibus patulis supra planis subtus prominentibus, venulis reticulatis; inflorescentia prope apices ramulorum axillari breviter racemosa 3–7-flora; rhachide gracili 5–12 mm. longa parce strigosa. basi bracteata; pedicellis gracilibus 3–6 mm. longis dense ferrugineo-strigosis, bracteis ovatis glabris circiter 2.5 mm. longis et 2 mm. latis subtentis, prope basin bracteolis similibus minoribus bibracteolatis; calyce campanulato, pilis ferrugineis 1 mm. longis dense strigosis, distaliter glabrescente, lobis 5 deltoideis acutis, sub anthesi circiter 3 mm. longis et 2 mm. latis; corolla breviter cylindrica, maturitate 5–6 mm. longa et 3–4 mm. diametro, superne contracta, velut calyce strigosa, lobis 5 deltoideis subacutis circiter 1 mm. longis et latis; staminibus 10, 3.5 mm. longis; filamentis stramineis, glabris vel parce pallide pilosis, circiter 2.2 mm. longis et basi 0.6 mm. latis, superne contractis; antheris submembranaceis, aristis inclusis 1.5 mm. longis, per poros ovales apicales dehiscentibus; ovario depresso-globoso, sub anthesi 1.5–2.5 mm. diametro, pilis minutis dense molliter induto; stylo crasso circiter 3 mm. longo, stigmate minute lobato.

Type, *Purdie*, collected in the Quindio region of Colombia and deposited in the herbarium of the Royal Botanic Gardens, Kew. Duplicate at Y. The indument of the new species is strikingly similar to that of *G. strigosa* Benth., from which the small revolute leaves and shorter inflorescences serve to distinguish it.

GAULTHERIA BRACTEATA (Cav.) G. Don Gen. Syst. 3: 840. 1834. *Andromeda bracteata* Cav. Ic. 6: 42. pl. 562, f. 1. 1801. *Gaultheria pichinchensis* Benth. Pl. Hartw. 225. 1846. This species has not been well understood. In the Delessert herbarium there is a sheet bearing this inscription: "*Andromeda bracteata* Ic. tab. 562, ex montibus Chimborazo et Tunguragua. *Gaultheria erecta*? Vent. Hort. Cels. Exempleaire type envoye par Cavanilles." This is doubtless a fragment of the actual type of *G. bracteata*. A comparison of this specimen with the type of *G. pichinchensis* leaves no doubt of their similarity. The species is characterized by the dense ferruginous villose hairs of young branchlets and lower surfaces of leaves. It grows over a wide range at altitudes of 3000–4000 meters, and is represented by:

VENEZUELA: Merida: *Linden* 407 (C). Sierra Nevada, *Funck & Schlim* 1070 (C).

COLOMBIA: *Purdie* (K). Norte de Santander: Eastern slope of Páramo de Santurbán, *Killip & Smith* 19610 (Y). El Cauca: Páramo de la Unión, *André* 2930 (K, Y). Mt. Pan de Azucar, *Pennell* 7032 (B, K, Y). Paletara, *Pennell* 6951 (Y). Nariño: Alto de Arando, *Triana* 2643 (B, C, K).

ECUADOR: *Jameson* (C). *Fraser* (BM, C). *Sodiño* (B). "Mt. Chimborazo and Tunguragua," *Collector?* (C, type coll.). Pichincha: Mt. Pichincha, *Hartweg* 1228 (B, BM, C, K, type of *G. pichinchensis*); *Hall* (B), 72 (K); *André* 3862 (K), *K.* 777 (K); *Jameson* (K), 157 (K); *Lehmann* 488 (BM). Vicinity of Quito, *Jameson* (B, C, K), 310 (BM, C, K). Tunguragua: Mt. Tunguragua, *Spruce* 5156 (BM, C, K). Chimborazo: Mt. Chimborazo, *Wymper*, (BM).

PERU: Huanuco: Monzon, *Weberbauer* 3377 (B).

Gaultheria vegasana sp. nov. Frutex 1–3 m. altus; ramis ramulisque subteretibus fuscis, arcte puberulis et pilis ferrugineis glandulosis ad 1.5 mm. longis plus minusve persistentibus setosis; petiolis rugosis setosis 2–5 mm. longis; laminis subcoriaceis ovatis, 2.5–4 cm. longis, 1.8–2.2 cm. latis, basi rotundatis, apice acutis et calloso-mucronatis, margine leviter revolutis subintegris vel crenulatis, supra maturitate subglabris et nervis puberulis, subtus pilis villosis ferrugineis ad 2.5 mm. longis indutis, pinnatinerviis, nervis secundariis plerumque 3-jugis adscendentibus, cum costa supra planis vel leviter impressis subtus elevatis, venulis reticulatis planis vel leviter elevatis; inflorescentia axillari racemosa 10–16-flora; rhachide 2.5–3 cm. longa, parce puberula ac etiam pilis densis ferrugineis glandulosis circiter 1 mm. longis praedita, basi bracteata; pedicellis 4–5 mm. longis velut rhachide puberulis et villosis, bracteis subcoriaceis obovatis subtentis (bracteis 5–7 mm. longis, 3–5 mm. latis, extra et margine dense glanduloso-villosis, intus glabris), bracteolis

linearibus villosis circiter 3 mm. longis bibracteolatis; floribus pilis paucis decidue glandulosis ad 0.5 mm. longis setosis; calycis lobis deltoideo-ovatis acutis sub anthesi 1.5–2 mm. longis et 1.5 mm. latis; corolla campanulato-cylindrica maturitate circiter 5 mm. longa et 4 mm. diametro, lobis obtusis circiter 0.8 mm. longis; staminibus 10, circiter 3.5 mm. longis; filamentis stramineis ligulatis 2–2.5 mm. longis, pilos delicatulos gerentibus; antheris aristis brevibus inclusis circiter 1.5 mm. longis; ovario depresso-globoso sub anthesi 2–2.5 mm. diametro, minute villoso; stylo carnosio circiter 3 mm. longo apice incrassato, stigmatе truncato.

Type, *Killip & Smith 15825*, collected Dec. 20 or 21, 1926, along edge of woods in mountains east of Las Vegas, Department of Santander, Colombia, alt. 3000–3300 meters, and deposited in the herbarium of the New York Botanical Garden. Duplicate at N. Field notes indicate that the calyx lobes are red and the corolla pinkish white. It is related to *G. bracteata* (Cav.) G. Don, from which species it differs in the shape of the bracts, which are dorsally glandular-pilose rather than glabrous, and in the sparsely setose rather than glabrous corollas. It is also to be compared with *G. vestita* Benth., a species with more exaggerated pubescence of branchlets and inflorescence and with the leaves cordate at base.

Gaultheria santanderensis sp. nov. Frutex parvus ad 2 m. altus vel saepe subprostratus; ramulis subteretibus, juventute pallide puberulis ac etiam pilis paucis brevibus glandulosis setosis, mox glabrescentibus; petiolis crassis subrugosis decidue puberulis 2–4 mm. longis; laminis coriaceis late ovatis, 2.5–4.5 cm. longis, 2–3.5 cm. latis, basi cordatis, apice subacutis et calloso-mucronatis, margine serrulatis (dentibus circiter 15 per centimetrum), supra juventute parce puberulis mox glabris et nitidis, subtus pilis tomentosis densis gracilibus stramineis ad 1 mm. longis indutis demum glabrescentibus, pinnatinerviis, nervis secundariis plerumque 3-jugis arcuatis, cum costa supra impressis subtus elevatis, venulis copiose reticulatis; inflorescentia prope apices ramulorum axillari, racemosa 8–16-flora; rhachide 1.5–4.5 cm. longa, arcte puberula ac etiam pilis densis gracilibus stramineis glandulosis ad 1 mm. longis setosa, basi bracteata; pedicellis 7–13 mm. longis velut rhachide puberulis et setosis, bracteis ovatis decidue setosis 6–10 mm. longis subtentis, bracteolis similibus deciduis circiter 4 mm. longis bibracteolatis; floribus partibus exterioribus ubique tomentosis, pilis ferrugineis 0.5–1.5 mm. longis saepe minute glandulosis; calycis lobis 5 elongato-deltoideis acutis, sub anthesi 4–5 mm. longis et basi 3 mm. latis; corolla late cylindrica, maturitate 8–9 mm. longa et circiter 5 mm. diametro, lobis 5 obtusis circiter 1 mm. longis; staminibus 10, circiter 6 mm. longis; filamentis stramineis ligulatis 4–4.5 mm. longis et prope basin ad 1 mm. latis, pilos delicatulos circiter 0.3 mm. longos gerentibus; antheris oblongis, aristis circiter 0.5 mm. longis inclusis 3–3.5 mm. longis; ovario subgloboso sub anthesi 2.5–3 mm. diametro, minute puberulo; stylo carnosio circiter 5 mm. longo, stigmatе truncato.

Type, *Killip & Smith 17303*, collected Jan. 16–20, 1927, on open rocky hillside near Vetás, Department of Santander, Colombia, alt. 3100–3250 meters, and deposited in the herbarium of the New York Botanical Garden. Duplicate at N. Other Colombian collections, at an altitude of 3000–3800 meters and by the same collectors unless otherwise noted, are: Norte de Santander: Páramo de Pamplona, *Purdie* (K). Santander: Páramo Rico, near Vetás, 17663 (N, Y). Western slope of Páramo Rico, 17215 (N, Y), 17745 (N, Y). Páramo de las Vegas, 15681 (N, Y). Field notes indicate that the calyx becomes deep red with age, the corolla varying from pale to deep pink.

It is a very distinct species, readily distinguished from others of Colombia by the soft tomentum of the leaves, and by its unusually large and densely pubescent flowers. Its relationship is probably with *G. vestita* Benth., which species has much smaller and shorter-petioled flowers. The leaves of *G. vestita* are setose beneath, while those of *G. santanderensis* usually bear softer hairs. However, of the above-cited specimens, nos. 15681 and 17745 show a tendency towards setose pubescence. In inflorescence *G. santanderensis* may be compared with the Ecuadorean *G. lanigera* Hook., than which species it has leaves more than twice as large, differently shaped, and plane rather than conspicuously revolute at margins.

***Gaultheria Pennellii* sp. nov.** Frutex ramosus; ramulis teretibus, juventute pilis ferrugineis nigrescenti-glandulosis circiter 2 mm. longis dense setosis, demum glabrescentibus; petiolis subrugosis 3–5 mm. longis, velut ramulis setosis; laminis coriaceis oblongis, 3.5–5 cm. longis, 1.7–3.5 cm. latis, basi subcordatis, apice subacutis et calloso-mucronatis, margine crenulatis, supra subglabris et nitidis, subtus et margine pilis setosis glandulosis deciduis 0.5–1 mm. longis indutis, pinnatinerviis, nervis secundariis 3- vel 4-jugis arcuato-adscendentibus, cum costa supra impressis subtus prominentibus, venulis copiose reticulatis; inflorescentia prope apices ramulorum axillari racemosa, 10–16-flora; rhachide gracili 3–4 cm. longa, basi bracteata, dense setosa (pilis ferrugineis nigrescenti-glandulosis ad 0.8 mm. longis) ac etiam minute pallide puberula; pedicellis gracilibus 5–10 mm. longis, velut rhachide setosis et puberulis, bracteis coriaceis oblongis circiter 5 mm. longis (bracteis ciliis crassis glandulosis vel laxis pallidis fimbriatis) subtentis, prope medium bracteolis minoribus similibus bibracteolatis; calyce tenuiter coriaceo, juventute velut pedicello pubescente demum glabrescente, lobis 5 deltoideis, sub anthesi circiter 2 mm. longis et 1.5 mm. latis, acuminatis, margine persistenter fimbriatis; corolla rubra tenuiter carnosa breviter cylindrica, maturitate 4.5–5 mm. longa et 3–3.5 mm. diametro, pilis circiter 0.8 mm. longis glanduloso-setosa, lobis 5 deltoideis subacutis, circiter 1 mm. longis et latis; staminibus 10, 3–3.5 mm. longis; filamentis pallide castaneis circiter 2.3 mm. longis laxe pilosis; antheris aristis brevibus inclusis circiter 1.3 mm. longis, per poros

latos dehiscentibus; ovario depresso-globoso, sub anthesi circiter 1.5 mm. diametro, glabro vel parce pilosulo; stylo circiter 3 mm. longo, stigmate subtruncato.

Type, *Pennell 4341*, collected Feb. 24, 1918, in shrub zone below Páramo de Chaquiro, Cordillera Occidental, Department of Bolívar, Colombia, alt. 2800–3100 meters, and deposited in the herbarium of the New York Botanical Garden. Other collections, from the neighboring Department of Antioquia, are: Alto San José, alt. about 3000 meters, *Kalbreyer 1587* (B, K); vicinity of Medellín, *R. R. White* (K). It is a species allied to *G. vestita* Benth., which has the pubescence, especially of calyces, more pronounced and persistent than the new species. *G. vestita* has the calyx lobes pilose within, the ovary densely pilose, the leaves proportionately broad, and the petioles very short, in which characters it contrasts with *G. Pennellii*.

Gaultheria hapalotricha sp. nov. Frutex subprostratus nanus (specimina nostra ad 20 cm. alta); ramulis teretibus, juventute pilis ferrugineis decidue glandulosis ad 2 mm. longis setosis mox glabrescentibus; petiolis teretibus decidue setosis 2–3 mm. longis; laminis coriaceis olivaceis obovatis, 2.5–3.5 cm. longis, 1.7–2.5 cm. latis, basi acutis vel subattenuatis, apice rotundatis et calloso-apiculatis, margine integris et leviter incrassatis, utrinque pilis ferrugineis decidue glandulosis circiter 1 mm. longis adscendentibus vel patulis indutis, demum glabrescentibus, pinnatinerviis, nervis secundariis plerumque 3-jugis rectis adscendentibus, e costa prope basin orientibus, cum costa supra leviter impressis subtus elevatis, venulis inconspicue reticulatis; inflorescentia prope apices ramulorum axillari, breviter racemosa, 6–12-flora; rhachide 5–12 mm. longa parce setosa, basi bracteata; pedicellis gracilibus 3–6 mm. longis, pilis stramineis patulis densis circiter 0.4 mm. longis praeditis, bracteis subcoriaceis decidue puberulis oblongis 5–6 mm. longis subtentis, bracteolis similibus 3–4 mm. longis decidue bibracteolatis; calyce pilis pallidis nigrescenti-glandulosis circiter 0.8 mm. longis praedito, lobis 5 ovato-deltoides acuminatis minute pallide ciliolatis, sub anthesi circiter 3 mm. longis et 2 mm. latis; corolla breviter cylindrico-urceolata molliter carnosae, maturitate 6–7 mm. longa et 3.5–4.5 mm. diametro, superne contracta, velut calyce parce pilosa, lobis 5 ovato-deltoides obtusis; staminibus 10, 4.5–5 mm. longis; filamentis stramineis ligulatis circiter 4 mm. longis et prope basin 0.5 mm. latis, superne contractis, pilis pallidis delicatulis circiter 0.3 mm. longis parce pilosis; antheris castaneis membranaceis, aristis brevibus inclusis 0.8–1 mm. longis, per poros ovales subapicales dehiscentibus; ovario subgloboso sub anthesi 1.5–2 mm. diametro, minute puberulo; stylo carnosio circiter 2.7 mm. longo, stigmate subtruncato.

Type, *Killip & Smith 19626*, collected Feb. 20, 1927, on sandy soil at edge of woods on the eastern slope of Páramo de Santurbán, toward

Mutiscua, Department of Norte de Santander, Colombia, alt. 3600–3900 meters, and deposited in the U. S. National Herbarium (no. 1,354,823). Another collection is *Tracey 485* (K), collected on Páramo de Choachi, Department of Cundinamarca, alt. 3100 meters. The fact that only these two widely separated stations are known indicates the sparsely collected character of the intervening páramos. It is a very distinctive species, probably best grouped with *G. odorata* Willd. and its allies, with which it has in common a pilose corolla. However, our species is readily distinguished by its dwarfed habit, its obovate acute-based leaves with ascending veins, and its acuminate calyx lobes. The calyx is bright pink without and pale pink or white within. The hairs of pedicel and calyx, when these organs are boiled, are seen to be extraordinarily delicate and pale, bearing minute black glands. The corolla is pale pink and of an unusually delicate texture, as are the pale slender filaments.

Gaultheria psilantha sp. nov. Frutex ramosus; ramulis subteretibus striatis fuscis glabris; petiolis subrugosis incrassatis glabris 1.5–3 mm. longis; laminis coriaceis margine excepto glabris oblongis, 3.5–5.5 cm. longis, 2–3 cm. latis, basi truncatis vel subcordatis, apice acutis et calloso-mucronatis, margine serratis (dentibus 6–9 per centimetrum, ciliis rigidis deciduis 1–1.5 mm. longis terminatis), pinnatinerviis, nervis secundariis 3- vel 4-jugis, arcuato-adscentibus, cum costa supra elevatis subtus prominentibus, venulis copiose reticulatis utrinque elevatis; inflorescentia apices ramulorum versus axillari racemosa 10–22-flora; rhachide crassa 2–7 cm. longa minute pallide puberula basi bracteata; pedicellis subteretibus 5–10 mm. longis minute pallide puberulis, bracteis coriaceis subglabris oblongis acutis 5–8 mm. longis subtentis, prope basin bracteolis minoribus similibus bibracteolatis; calyce subcoriaceo subglabro (margine decidue pallide puberulo), lobis 5 ovato-deltoides acutis, sub anthesi 4–4.5 mm. longis et 2.5–3 mm. latis; corolla pallide rubescente tenuiter carnosa glabra breviter cylindrica, maturitate circiter 8 mm. longa et 4 mm. diametro, lobis 5 deltoideis obtusis, circiter 1.5 mm. longis et latis; staminibus 10 circiter 5 mm. longis; filamentis stramineis minute puberulis, 3–3.5 mm. longis, basi circiter 0.8 mm. latis, superne contractis; antheris fusco-castaneis submembranaceis, aristis circiter 0.5 mm. longis inclusis 2–2.3 mm. longis, per poros latos dehiscentibus; ovario subgloboso, sub anthesi circiter 2.5 mm. diametro, minute pallide piloso; stylo crasso quam corolla paullo brevior.

Type, *Pennell 2067*, collected Sept. 20, 1917, on the dry and grassy Páramo de Cruz Verde, near Bogotá, Department of Cundinamarca, Colombia, alt. 3400–3600 meters, and deposited in the herbarium of the New York Botanical Garden. Other collections, also from Cundinamarca, are: Páramo de Choachi, alt. 3300 meters, *Tracey 486* (K); a páramo near

Bogotá, *Schultze 24* (B). The latter specimen has the pedicels subtended by lanceolate-oblong bracts up to 12 mm. long. It is of the relationship of *G. rigida* HBK., from which species it differs by having the leaf venation coarser and more obvious, the inflorescence more robust in all parts, and the texture of bracts, calyces and corollas more coriaceous.

Gaultheria antioquiensis sp. nov. Frutex; ramulis teretibus fuscis, juventute minute pallide puberulis demum glabrescentibus; petiolis subrugosis subteretibus 4–7 mm. longis, velut ramulis puberulis; laminis coriaceis olivaceis (vel subtus rubentibus) oblongo-ovatis, 6–9 cm. longis, 2.5–4 cm. latis, basi acutis vel subobtusis saepe petiolis decurrentibus, apice subacutis callosomucronatis, margine serrato-crenatis (dentibus 12–14 per centimetrum nigro-apiculatis), supra maturitate glabris, subtus conspicue glanduloso-punctatis, pinnatinerviis, nervis secundariis 3- vel 4-jugis adscendentibus, cum costa supra impressis subtus prominentibus, venulis reticulatis supra obscuris subtus elevatis; inflorescentia axillari racemosa 15–25-flora; rhachide gracili tereti, dense albo-puberula ac etiam parce fusco-glanduloso-pilosa (pilis circiter 0.3 mm. longis), basi bracteis arcte imbricatis dense circumdata; pedicellis gracilibus 3–6 mm. longis, velut rhachide puberulis et parce glandulosis, bracteis subcoriaceis prominenter striatis oblongo-spatulatis 10–15 mm. longis subtentis (bracteis juventute puberulis, margine glanduloso-pilosis, apice acutis), bracteolis patulis similibus linearibus 3–4 mm. longis prope basin bibracteolatis; calyce parce puberulo vel glabro, lobis 5 deltoideis acutis, sub anthesi 2–3 mm. longis et 2 mm. latis; corolla breviter cylindrico-urceolata submembranacea glabra, maturitate 6 mm. longa et 4–5 mm. diametro, lobis 5 deltoideis obtusis; staminibus 10, 3.5–4 mm. longis; filamentis stramineis ligulatis circiter 2.5 mm. longis et prope basin 0.5 mm. latis; antheris membranaceis, aristis inclusis circiter 1.3 mm. longis; ovario depresso-globoso subglabro sub anthesi 2.5 mm. diametro; stylo circiter 3 mm. longo, stigmate subtruncato.

Type, *R. A. Toro 984*, collected Feb. 1, 1928, at Tamesis, near Medellín, Department of Antioquia, Colombia, and deposited in the herbarium of the New York Botanical Garden. Other collections, also from Antioquia, are: San José, *Kalbreyer 1586* (B, K); Santa Elena, *Archer 635* (N). It is a species allied to *G. rigida* H.B.K., from which it differs by having the leaves acute rather than cordate at base. The densely glandular-punctate lower leaf surfaces, the conspicuously striate bracts, and the slender spreading bractlets are also characteristic of the new species.

Gaultheria microdonta sp. nov. Frutex compactus; ramis ramulisque subteretibus fuscis mox cinerascentibus, juventute minute puberulis ac etiam pilis castaneis 0.6 mm. longis setosis, demum glabrescentibus; petiolis rugosis decidue setosis 2–3 mm. longis; laminis coriaceis olivaceis oblongis, 20–28 mm. longis, 7–12 mm. latis, basi rotundatis vel subtruncatis, apice subacutis et

calloso-mucronatis, margine leviter incrassatis et serrulatis (dentibus circiter 15 per centimetrum, ciliis rigidis deciduis terminatis), supra glabris, subtus pilis stramineis patulis 1–1.5 mm. longis setosis, pinnatinerviis, costa supra impressa subtus elevata, nervis secundariis 3- vel 4-jugis brevibus, venulis reticulatis supra subplanis subtus leviter elevatis; inflorescentia prope apices ramulorum axillari, racemosa 8–15-flora; rhachide gracili 1.5–2 cm. longa, velut ramulis puberula et setosa, basi bracteis parvis circumdata; pedicellis gracilibus 4–8 mm. longis puberulis et setosis (setis minute glandulosis), bracteis subglabris lanceolato-oblongis 4–6 mm. longis subtentis, bracteolis similibus 3.5–4 mm. longis decidue bibracteolatis; calyce carnoso minute albo-puberulo, lobis 5 deltoideis acutis sub anthesi circiter 3.5 mm. longis et 2 mm. latis; corolla tenuiter carnosa subcylindrica, maturitate 6–7 mm. longa et 3–4 mm. diametro, superne contracta, velut calyce puberula, lobis 5 obtusis circiter 1 mm. longis; staminibus 10, circiter 4 mm. longis; filamentis stramineis ligulatis circiter 2.5 mm. longis, pilos delicatulos circiter 0.3 mm. longos gerentibus; antheris membranaceis, aristis inclusis 1.5–2 mm. longis, per poros ovaes subapicales dehiscentibus; ovario subgloboso sub anthesi circiter 2 mm. diametro, dense puberulo; stylo 3.5–4 mm. longo, stigmatibus truncato.

Type, *Brother Ariste-Joseph A301*, collected in October, 1907, at Montserrat, Department of Cundinamarca, Colombia, and deposited in the U. S. National Herbarium (no. 1,067,860). It is a species most closely related to *G. brachybotrys* DC., from which it differs by the smaller leaves which are less conspicuously pilose beneath, the narrower inflorescence bracts, the longer calyx lobes, and the pale-puberulous rather than glabrous corollas.

Gaultheria alnifolia (Dun.) comb. nov. *Thibaudia alnifolia* Dun.; DC. Prodr. 7: 564. 1839. *Gaultheria Lindeniana* Planch. Fl. des Serres I. 5: 501D. 1849. *Proclesia alnifolia* Kl. Linn. 24: 35. 1851. *Chupalon alnifolium* Ktze. Rev. Gen. Pl. 2: 384. 1891. *Cavendishia alnifolia* Hoer. Bot. Jahrb. Engl. 42: 273. 1909. The present species is readily distinguished from others of the region by its reddish-brown leaves and branchlets, and by the obovate leaves, which are attenuate at base and rounded or apiculate at apex. It is well described and figured by Planchon, of whose species *Linden 36* is probably the type collection. The type specimen of Dunal's species is sterile, but its position here is unmistakable. It is represented by:

VENEZUELA: without definite locality: *Karsten 9* (B). Las Lagunetas, *Moritz 1591* (BM). Miranda: El Cedral de las Ajuntas, near Los Teques, 1000–1800 m., *Pittier 6115* (B, Y). Federal District: Caracas and vicinity, *Vargas* (C, type); *Linden 36* (BM, C, K, P, type of *G. Lindeniana*), *315* (P); *Birschel* (K); *Funck 354* (C, P); *Funck & Schlim 122* (BM, C, P); *Gollmer* (B); *Allart 99* (C, Y). Aragua: Colonia Tovar, *Fendler 740* (C, K, Y); *Moritz 353* (B, BM, C).

VACCINIACEAE

Vaccinium Benthamianum nom. nov. *Anthopterus mucronatus* Benth. Pl. Hartw. 221. 1846; not *Vaccinium mucronatum* L. (1753). *Thibaudia mucronata* Hoer. Bot. Jahrb. Engl. 42: 274. 1909. Examination of the type of *Anthopterus mucronatus* indicates that it is a species of *Vaccinium* of the alliance of *V. polystachyum* Benth., from which it differs by having the calyx obviously angled, the inflorescence slightly longer, and the leaves entire and revolute at margins and conspicuously mucronate at apex. It is represented by:

COLOMBIA: Tolima: Quindio region, 2800–3450 m., *Triana 2656* (BM, C, K, P, Y); *André 2218* (K, Y). El Cauca: Cordillera Pitayo, near Popayan, *Hartweg 1210* (BM, K, type).

Allied to *V. Benthamianum* are two recently collected species here described. The three species, which form a distinct group within the genus, may be distinguished from one another thus:

Flowers solitary or in pairs; pedicels 3–4 mm. long; calyces and young corollas brown-pilose; calyx limb distinctly lobed..... *V. anfractum*
 Flowers glabrous, short-racemose, 2–4 per inflorescence; pedicels 5–8 mm. long; calyx limb short-apiculate..... *V. Pennellii*
 Flowers glabrous, racemose, 8–15 per inflorescence; calyx limb distinctly lobed..... *V. Benthamianum*

Vaccinium anfractum sp. nov. Frutex parvus; ramulis subpendulis teretibus anfractis, juventute pilis ferrugineis ad 0.4 mm. longis villosis; petiolis rugosis villosis 1–2 mm. longis; laminis coriaceis ovatis, 15–20 mm. longis, 7–11 mm. latis, basi rotundatis vel obtusis, apice acutissimis callosis, margine integris subcartilagineis, utrinque glabris vel parce breviter glanduloso-setosis, e basi obscure 3–5-nerviis, costa utrinque plana vel supra impressa, nervis secundariis et venulis obscuris; floribus axillaribus solitariis vel binis; pedicellis subrugosis rectis parce villosis 3–4 mm. longis, cum calyce continuis, prope basin bracteolis ovatis ad 0.8 mm. longis bibracteolatis; calyce coriaceo, pilos patulos ferrugineos circiter 0.5 mm. longos gerente, tubo obprismatico 5-angulato sub anthesi circiter 3 mm. longo et 2.5 mm. diametro, limbo suberecto, lobis inclusis 1.5 mm. longo, lobis 5 deltoideis acutis circiter 0.8 mm. longis; corolla molliter carnea parce villosa vel glabra cylindrica, 8–10 mm. longa, 3–3.5 mm. diametro, 5-lobata, lobis oblongis subacutis circiter 1.5 mm. longis; staminibus 10 aequalibus quam corolla paullo brevioribus; filamentis distinctis ligulatis circiter 4 mm. longis superne pilosis; antheris membranaceis tubulis inclusis circiter 5 mm. longis, tubulis quam loculis paullo longioribus, per rimas ad 1.5 mm. longas dehiscentibus; stylo corollam subaequante, stigmate subcapitato.

Type, *Pennell 7446*, collected June 29 or 30, 1922, in shrub-zone ("paramillo") on Mt. Santa Ana, Department of El Cauca, Colombia, alt. 2700–3000 meters, and deposited in the herbarium of the New York Botanical Garden. It is a species without close relatives in the northern Andes other than the following new species, from which it is readily distinguished as noted in the above key.

Vaccinium Pennellii sp. nov. Frutex parvus plus minusve decumbens; ramulis subteretibus juventute parce puberulis mox glabrescentibus; petiolis rugosis subglabris 1.5–2.5 mm. longis; laminis coriaceis ovatis, 15–23 mm. longis, 7–11 mm. latis, basi obtusis vel truncatis, apice obtusis sed mucronatis, margine leviter revolutis, subintegris vel crenulatis, utrinque glabris et parce punctatis, e basi obscure 3–5-nerviis, costa supra impressa subtus elevata, nervis secundariis adscendentibus supra leviter impressis, venulis obscuris; inflorescentia axillari breviter racemosa glabra 2–4-flora; rhachide 2–5 mm. longa, basi minute bracteata; pedicellis gracilibus subrugosis 5–8 mm. longis, cum calyce continuis, bracteis anguste ovatis ad 1 mm. longis subtentis, infra medium bracteolis similibus bibracteolatis; calycis tubo obprismatico 5-angulato sub anthesi 3–3.5 mm. longo et diametro, limbo erecto lobis inclusis 1.5–2 mm. longo, lobis 5 breviter apiculatis; corolla cylindrica apice contracta, 8–9 mm. longa, 4–5 mm. diametro, 5-lobata; staminibus 10 aequalibus quam corolla paullo brevioribus; filamentis distinctis stramineis ligulatis glabris circiter 3.5 mm. longis; antheris tubulis inclusis 5.5–6 mm. longis, tubulis elongato-conicis flexilibus quam loculis paullo longioribus, per rimas 1–2 mm. longas dehiscentibus; stylo corollam subaequante, stigmathe subtruncato.

Type, *Pennell 10522*, collected Sept. 8–10, 1922, in shrub zone below páramo on Cerro Tatama, Department of Caldas, Colombia, alt. 3300–3500 meters, and deposited in the herbarium of the New York Botanical Garden. Other collections, also from Colombia, are: Bolivar: below Páramo de Chaquiro, 2800–3100 m., *Pennell 4316* (Y). Bolivar-Antioquia Boundary: Páramo de Chaquiro, 3000–3200 m., *Pennell 4288* (Y). Tolima: Cerro Pelado, 2684 m., *Stuebel 249b* (B).

Ceratostema Pearcei (Britton) comb. nov. *Rusbya Pearcei* Britton, Bull. Torr. Club 20: 68. 1893. *Anthopterus Pearcei* Drude; Engl. & Prantl, Pflanzenfam. Nachtr. 4¹: 270. 1897. The present species was excluded from the genus *Rusbya* in a recent paper,¹ but until the present I have not been able to place it with accuracy. Examination of the type specimen indicates that it is a *Ceratostema*, most closely allied to *C. buxifolium* Field. & Gardn., from which it differs by having the leaves uniformly larger and subacute rather than rounded at apex. A more detailed description than the original is here published:

¹ Contr. U. S. Nat. Herb. 28: 446. 1932.

Compact epiphytic shrub; branchlets cinereous, striate, sparsely puberulous when young, glabrescent, swollen at petioles; stipules lanceolate, 3–5 mm. long, deciduous; petioles violaceous, slender, about 1 mm. long; leaf blades subcoriaceous, oblong, 15–22 mm. long, 5–9 mm. broad, rounded at base, subacute at apex, entire at margins, glabrous above, sparsely and deciduously pilose beneath with minute stiff nigrescent hairs, obscurely pinnate-veined, the secondary veins 1 or 2 per side, oriented near base; flowers axillary, solitary or in pairs, essentially glabrous in all parts; pedicels slender, subrugose, 6–12 mm. long, circumscribed at base by several minute subpuberulous bractlets, continuous with calyx; calyx tube obconical, subrugose, 2–3 mm. long, about 2 mm. in diameter at summit, 5-angled or narrowly 5-winged, the limb subspreading, about 2 mm. long including lobes, the lobes 5, ovate-deltoid, 1–1.5 mm. long, acute, deciduously pilose at margins; corolla thin-carnose, subcylindric, 6–8 mm. long, about 3 mm. in diameter, the lobes 5, deltoid, minute; stamens alternately slightly unequal, nearly as long as corolla; filaments castaneous, 1.5–2 mm. long, minutely pilose at margins; anther sacs slightly granular, about 2 mm. long; tubules flexible, 4–4.5 mm. long, opening by elongate clefts; style about as long as corolla, the stigma truncate.

BOLIVIA: La Paz: Pintac, 3100–3400 m., *Pearce* (K, type). Sandillani, 2500–2800 m., *Pearce* (K). Cochabamba: Incachaca, 2300 m., *Steinbach 8986* (Y).

Semiramisia fragilis sp. nov. Frutex gracilis epiphyticus; ramulis subteretibus juventute pallide puberulis mox cinerascentibus glabrescentibus; petiolis subglabris subteretibus rugosis 1.5–2 mm. longis; laminis coriaceis ovato-suborbicularibus, 15–28 mm. longis, 11–18 mm. latis, basi apiceque rotundatis, margine integerrimis crassis et leviter recurvatis, pilis rigidis adpressis deciduis parce indutis, supra nitidis subtus opacis, obscure 5-pli-nerviis, nervis secundariis prope basin orientibus adscendentibus, cum costa supra leviter elevatis subtus immersis, venulis obscuris; floribus axillaribus ut videtur solitariis; pedicellis gracilibus flexuosis 15–20 mm. longis, pilis pallidis patulis ad 0.5 mm. longis indutis, prope medium decidue bibracteolatis (bracteolis oblongis circiter 0.7 mm. longis), cum calyce continuis; calyce ut pedicello dense piloso, tubo obconico sub anthesi circiter 2 mm. longo et 1.5 mm. diametro, limbo suberecto, lobis inclusis 1–1.5 mm. longo, lobis 5 ovato-deltoides subacutis circiter 1 mm. longis et latis; corolla tenuiter carnosa dense pilosa (pilis pallidis circiter 0.3 mm. longis), cylindrico-urceolata, 23–24 mm. longa, prope basin 4–5 mm. diametro superne contracta apice patula, 5-lobata, lobis ovatis subacutis, circiter 1.5 mm. longis, 2.5 mm. latis; staminibus 10 aequalibus corollam aequantibus; filamentis distinctis (leviter cohaerentibus et basi seriebus duabus imbricatis), castaneis carnis glabris, 4–5 mm. longis, ad antheras connectivis brevibus gracilibus annexis; loculis leviter granulatis basi subacutis 2–3 mm. longis; tubulis membranaceis gracilibus (superne 0.25 mm. diametro), 17–18 mm. longis, per rimas obliquas 0.5 mm.

longas dehiscentibus; stylo leviter exserto filiformi superne incrassato, stigmate truncato.

Type, *Lehmann K.276*, collected in November, 1890, at Huahuidocal, West Andes of Cuenca, Province of Azuay, Ecuador, alt. 1800–2500 meters, and deposited in the herbarium of the Royal Botanic Gardens, Kew. Another Ecuadorean collection is: Río Amarollo, *André 4304* (F, K, Y). It is a species which in foliage and habit suggests *Oreanthes buxifolius* Benth., but the stamens are 10 rather than 5 and the calyx has neither the elongate tube nor lobes of *Oreanthes*. The facts that the short-lobed calyx is continuous with the pedicel and that the 10 stamens terminate in long slender tubules points to an alliance with *Semiramisia*. Here it is most suggestive of the Venezuelan *S. Karsteniana* Kl., but in the present species the calyx is small, the characteristic large campanulate corolla is much reduced, and the leaves are small and rounded at apex. It might well be considered generically distinct, but since the fundamental features are those of *Semiramisia*, it seems best to expand the concept of that genus to include the present species.

Psammisia caloneura sp. nov. Frutex; ramis ramulisque subteretibus fuscis minute fusco-puberulis glabrescentibus, internodiis bracteas (folias reductas?) hic illic gerentibus, bracteis submembranaceis lanceolato-oblongis sessilibus acutis 8–17 mm. longis, velut foliis minimis nervatis, nunc inflorescentiam subtentibus nunc solitariis; petiolis subteretibus decidue fusco-puberulis incrassatis, 3–7 mm. longis, 2.5–4 mm. diametro; laminis subcoriaceis ovato-oblongis, 18–30 cm. longis, 6.5–15 cm. latis, basi rotundatis vel late cuneatis, apice longe acuminatis, margine integerrimis, glabris (saepe nervis principalibus minute puberulis), pinnatinerviis, costa crassa supra plana vel elevata subtus prominentissima, nervis secundariis 12–20-jugis (nervis tertiariis fere aequè prominentibus alternantibus), subrectis patulis prope margines conspicue anastomosantibus, supra leviter impressis subtus prominentissimis, venulis crebre reticulatis, utrinque leviter elevatis; inflorescentia ramulis infra folia plerumque exoriente, saepe in axillis bractearum supra descriptarum, subfasciculata vel breviter racemosa (rhachide ad 5 mm. longa), ubique subglabra, 2–6-flora; pedicellis subrugosis nigrescentibus 6–13 mm. longis, bracteis coriaceis ovatis 1–1.5 mm. longis subtentis, prope basin decidue bibracteolatis; calycis tubo campanulato nigrescente sub anthesi 2.5–3 mm. longo et diametro, limbo coriaceo suberecto lobis inclusis circiter 2 mm. longo, lobis 5 ovatis apiculatis circiter 1 mm. longis et 2 mm. latis; corolla urceolata 8–9 mm. longa, prope basin circiter 4 mm. diametro superne contracta, lobis 5 oblongis subacutis circiter 1 mm. longis et latis; staminibus 10 aequalibus circiter 5.5 mm. longis; filamentis tenuiter carnosus castaneis distinctis, glabris vel intus superne parce puberulis, circiter 0.8 mm. longis, in connectivos angustiores productis, connectivis superne alternatim bicalcaratis,

calcaribus subacutis quam connectivis paullo latioribus; loculis basi incurvatis acutisque 2–2.5 mm. longis; tubulis cylindrico-conicis, circiter 2 mm. longis, per rimas breves dehiscentibus; stylo maturo exserto, stigmate subcapitato.

Type, *Triana 2690*, collected in May, 1853, between Barbacoas and Tuquerres, Department of Nariño, Colombia, alt. 900 meters, and deposited in the herbarium of the British Museum. Duplicates at K, P. It is a very distinct species which, in the numerous pinnate veins of its large leaves, bears but little resemblance to other Thibaudieae. I have not observed inter-nodal bracts, such as those above described, elsewhere in the tribe. The flowers are distinctly psammisioid, and the general appearance of the plant suggests *Psammisia Sodiroi* Hoer., which is doubtless its nearest relative. In addition to the characters above mentioned, *P. caloneura* is distinguished from *P. Sodiroi* by its fewer-flowered inflorescences and smaller flowers.

Thibaudia densiflora (Herzog) comb. nov. *Hornemannia densiflora* Herzog Med. Rijks. Herb. Leiden 27: 21. 1915. This species, originally placed in *Hornemannia* because of its alliance to *H. boliviensis* Ktze. (*Thibaudia boliviensis* (Ktze.) Hoer.), is more closely related to *T. regularis* A. C. Smith, from which it differs by having its broader leaves rounded rather than attenuate at base, its bractlets larger, and its calyces considerably more robust. The type collection (Bolivia: Incacorral, 2200 m., *Herzog 2250*) is represented at B and C.

Themistoclesia recurva sp. nov. Frutex gracilis (epiphyticus?); ramulis elongatis subteretibus gracilibus cinereis juventute parce puberulis; petiolis nigrescentibus rugosis 2–3 mm. longis decidue puberulis; laminis coriaceis anguste ovatis, 4.5–5.5 cm. longis, 1.5–2 cm. latis, basi rotundatis vel obtusis, apice acuminatis, margine integris et leviter recurvatis, utrinque subglabris, subtus decidue parce puberulis et fusco-strigosis, e basi obscure 3–5-nerviis, costa supra impressa subtus prominente superne obscure ramosa, nervis secundariis adscendentibus utrinque planis, venulis obscuris; inflorescentiis longe racemosis 1–3 in axillis foliorum, 6–12-floris; rhachide gracili flexili recurva 3–9 cm. longa, decidue cinereo-puberula; floribus glabris mox deciduis; pedicellis flexilibus subrugosis 15–20 mm. longis superne incrassatis, bracteis deciduis oblongis circiter 1 mm. longis subtentis, prope medium minute bibracteolatis, cum calyce continuis; calyce obconico, tubo carnosangulato, sub anthesi circiter 3 mm. longo et 2.5 mm. diametro, limbo patulo lobis inclusis 1–1.5 mm. longo, lobis apiculatis; corolla campanulata, 4.5–5 mm. longa, circiter 4 mm. diametro, lobis ovato-deltaideis, circiter 2 mm. longis et latis; staminibus subaequalibus circiter 3.5 mm. longis; filamentis nigrescentibus glabris circiter 1 mm. longis; antheris 2.7–3 mm. longis, tubulis latis loculos aequantibus, per rimas 0.8 mm. longas dehiscentibus; stylo crasso ad 4 mm. longo, stigmate truncato.

Type, *Pennell 9306*, collected Aug. 2–10, 1922, in forest at Pinares, above Salento, Department of Caldas, Colombia, alt. 2600–2800 meters, and deposited in the herbarium of the New York Botanical Garden. Other collections, also from Colombia, are: Tolima: *Goudot* (P). Pan de Azucar, 2800–3000 m., *Linden 920* (C, P). It is a species readily distinguished from others of the genus by its elongate recurved racemes, from which the scattered flowers are soon deciduous. The leaves are proportionately narrower than those of other species.

***Themistoclesia rostrata* sp. nov.** Frutex glaber gracilis (epiphyticus?); ramis ramulisque teretibus elongatis subscandentibus; petiolis rugosis circiter 2 mm. longis; laminis coriaceis ovatis, 7–10 cm. longis, 2.5–3.5 cm. latis, basi rotundatis vel leviter subcordatis, apice longe acuminatis (acumine ad 2 cm. longo), margine integris, utrinque glabris, 5-plex-nerviis, costa supra impressa subtus prominente, nervis secundariis prope basin orientibus adscendentibus, supra leviter impressis subtus planis vel elevatis, venulis plus minusve obscuris; inflorescentiis breviter racemosis 3–5 in axillis foliorum, 3-vel 4-floris; rhachide gracili 2–4 mm. longa; floribus mox deciduis, juventute partibus exterioribus parce ferrugineo-strigosis; pedicellis gracilibus 10–15 mm. longis, bracteis oblongis ad 1 mm. longis subtentis, infra medium minute bibracteolatis, cum calyce continuis; calyce obprismatico, tubo carnosangulato, 2.5–3 mm. longo et sub anthesi circiter 2.5 mm. diametro, limbo patulo lobis inclusis 1–1.5 mm. longo, lobis breviter apiculatis; corolla tenuiter carnosa subglobosa, 7–8 mm. longa, 4–6 mm. diametro, basi apiceque contracta, lobis deltoideis 1–1.5 mm. longis; staminibus subaequalibus 5–6 mm. longis; filamentis distinctis stramineis circiter 2 mm. longis, pilos patulos ad 0.5 mm. longos superne gerentibus; antheris tubulis inclusis circiter 5 mm. longis, tubulis latis loculos aequantibus, per rimas ovales ad 1 mm. longas dehiscentibus; stylo crasso quam corolla paullo brevior, stigmate truncato.

Type, *Pennell 2664*, collected Oct. 29, 1917, in forest below El Peñon, southwest of Sibaté, Department of Cundinamarca, Colombia, alt. 2600–2800 meters, and deposited in the herbarium of the New York Botanical Garden. Field notes indicate that the corolla is bright red, paler distally. Other collections, also from Cundinamarca, are: Fusagasuga, 2500 m., *Triana 2717* (C, P). Between Sibaté and Fusagasuga, *Linden 830* (C, P). Near Bogotá, *Goudot* (P). It is a species related to *T. pendula* Kl. and *T. dependens* (Benth.) A. C. Smith, from both of which it differs by its lax subscandent habit, its larger leaves, and its shorter distinctly subglobose corollas. The long-caudate leaves are well-spaced on the slender branchlets.

***Cavendishia coccinea* sp. nov.** Frutex gracilis; ramulis subteretibus juventute minute cinereo-puberulis demum glabrescentibus et fuscescentibus;

petiolis subglabris rugosis 4–6 mm. longis; laminis crasse coriaceis ovatis, 4–6 cm. longis, 1.5–2.5 cm. latis, basi acutis, apice longe caudato-acuminatis, margine integerrimis et leviter revolutis, glabris, supra nitidis, 5-ply-nerviis, costa supra plana vel impressa subtus elevata, nervis secundariis prope basin orientibus arcuatis, utrinque leviter elevatis, venulis reticulatis leviter elevatis vel obscuris; inflorescentia terminali vel axillari racemosa, 6–12-flora, basi bracteis parvis deciduis instructa; rhachide subtereti glabra 4–9 cm. longa; floribus glabris ut videtur in axillis bractearum alternarum solitariis, bracteis membranaceis glabris late ovatis, 2–3.5 cm. longis, 1.5–2.5 cm. latis, basi obtusis atque sessilibus, apice longe caudato-acuminatis (acumine 5–8 mm. longo), margine glandulosus (glandulis sessilibus, 6–8 per centimetrum, dentes minutos terminantibus), reticulato-nerviis; pedicellis subteretibus, 3–6 mm. longis, minute decidue bibracteolatis; calyce coriaceo subnigrescente, tubo campanulato, sub anthesi 2.5 mm. longo et 3 mm. diametro, limbo suberecto subcampanulato, lobis inclusis 4–5 mm. longo, lobis late deltoideis subacutis, 1.5 mm. longis, 3–4 mm. latis, glandulis coriaceis linearibus 1.5 mm. longis superne marginatis, sinibus rotundatis; corolla late cylindrica submembranacea, maturitate 30–35 mm. longa, circiter 6 mm. diametro, apice contracta, lobis 5 subnigrescentibus deltoideis 0.5 mm. longis; staminibus quam corolla paullo brevioribus; filamentis casteneis membranaceis, basi subcohaerentibus, glabris vel superne parce pilosis, alternatim 3 mm. et 9 mm. longis; loculis granulatis circiter 5 mm. longis; tubulis membranaceis amplis, alternatim 18–19 mm. et 13 mm. longis, per rimas elongatas dehiscentibus; stylo circiter 0.7 mm. diametro, stigmate truncato.

Type, *Triana 2698*, collected in February, 1853, at Acostadero, Cordillera del Chocó, Intendencia of El Chocó, Colombia, alt. 2500 meters, and deposited in the herbarium of the British Museum. Duplicates at C, K, P. Possibly *Jervise* (K), collected in Antioquia, without inflorescence, also represents the species. *C. coccinea* is another example of the remarkably distinct character of many plants of the Antioquia-El Chocó Andes. It has no close relatives, but may be compared with *C. adenophora* Mansf., with which it has in common an elongate calyx tube and glandular-margined bracts, but from which it differs in leaf shape and size, shape of bracts, method of inflorescence, size of flowers, etc. The delicate brilliant red bracts and large corollas of *C. coccinea* make its introduction to horticulture desirable.

Cavendishia rhynchophylla sp. nov. Frutex gracilis; ramulis subteretibus striatis decidue cinereo-puberulis; petiolis teretibus subnigrescentibus decidue puberulis 2–4 mm. longis; laminis coriaceis ovatis vel ovato-oblongis, 5–8 cm. longis, 2–3 cm. latis, basi rotundatis, apice longe caudato-acuminatis, margine integerrimis, subglabris, 5 (obscure 7)-ply-nerviis, nervis secundariis supra basin orientibus, arcuato-adscendentibus, cum costa supra fere planis

subtus elevatis, venulis copiose reticulatis, saepe supra elevatis; inflorescentia terminali vel axillari, racemosa, 8–15-flora, basi decidue bracteata; rhachide angulata glabra 3–6 cm. longa; pedicellis striatis parce puberulis 5–12 mm. longis, bracteis submembranaceis oblongis sessilibus subglabris ad 10 mm. longis subtentis, prope basin decidue minute bibracteolatis; florum partibus exterioribus ubique pilis uniformibus patulis cinereis 0.3–0.4 mm. longis pilosis; calycis tubo breviter cylindrico, sub anthesi circiter 1 mm. longo et 3 mm. diametro, superne constricto, limbo suberecto, lobis inclusis circiter 2.5 mm. longo, lobis deltoideis acutis, circiter 1 mm. longis, 3–4 mm. latis, apice callosis; corolla cylindrica maturitate 11–13 mm. longa, 4 mm. diametro, lobis deltoideis acutis circiter 1 mm. longis; staminibus quam corolla paullo brevioribus; filamentis castaneis glabris distinctis, alternatim 2 mm. et 4 mm. longis; loculis granulatis circiter 3 mm. longis; tubulis alternatim circiter 7 mm. et 6 mm. longis, per rimas elongatas dehiscentibus; stylo corollam aequante, stigmate truncato.

Type, *Triana 2676*, collected in July, 1853, at San Antonio, Western Cordillera, Department of El Valle, Colombia, alt. 1800 meters, and deposited in the herbarium of the British Museum. Duplicates at C, P, Y. It is a distinct species, probably most closely allied to *C. Lindauiana* Hoer., *C. hispida* A. C. Smith, and *C. callista* Donn. Sm., from all of which it is distinguished by smaller flowers and leaves and by pilose calyces. It may also be sought among the species allied to *C. cordifolia* (HBK.) Hoer., from which group it differs by its elongate inflorescence, long calyx limb, callose-tipped calyx lobes, and by various foliage aspects.

Cavendishia Gleasoniana sp. nov. Frutex; ramulis subteretibus striatis gracilibus violaceis glabris (juventute minute puberulis); petiolis crassis rugosissimis decidue pilosis 4–7 mm. longis; laminis oblongis coriaceis bullatissimis, 7–12 cm. longis, 4–5.5 cm. latis, basi cordatis, apice caudato-acuminatis (? specimine nostro incompleto), margine integerrimis et anguste revolutis, supra subglabris subtus pilosis, pilis setosis cinereis circiter 1 mm. longis, 5–7-plici-nerviis, nervis secundariis supra basin orientibus, jugo summo cum costa prope apicem rejuncto, jugis inferioribus arcuato-adscentibus, cum costa supra impressis subtus prominentibus, venulis copiose reticulatis utrinque elevatis; inflorescentia axillari breviter racemosa pauciflora, ubique glabra, basi bracteis imbricatis oblongo-ovatis papyraceis ad 2.5 cm. longis instructa; rhachide circiter 1 cm. longa; pedicellis subrugosis 5–8 mm. longis, basi bractea decidua eis basi rhachidis simili subtentis, prope basin decidue bibracteolatis, superne incrassatis et cum calyce articulatis; calycis tubo rugoso breviter cylindrico subapophysato, sub anthesi circiter 2 mm. longo et 3 mm. diametro, limbo erecto, cum lobis 3–4 mm. longo, lobis deltoideis, 1–1.5 mm. longis et latis, apice callosis; corolla submembranacea cylindrica, 20–25 mm. longa, circiter 4 mm. diametro; staminibus subaequalibus (filamentis anther-

isque compensanter inaequalibus), circiter 23 mm. longis; filamentis castaneis distinctis, brevioribus 2–3 mm. longis et glabris, longioribus gracilibus 6–8 mm. longis et superne parce pilosis; loculis leviter granulatis 5–8 mm. longis; tubulis flexilibus alternatim 15–18 mm. et 11–13 mm. longis, per rimas elongatas dehiscentibus; stylo filiformi corollam aequante, stigmate truncato.

Type, *Schomburgk*, collected in the vicinity of Mount Roraima, British Guiana, and deposited in the herbarium of the Royal Botanic Gardens, Kew. It allies itself to those *Cavendishias* with elongate calyx limb and callose-thickened lobes. It agrees with the Andean *C. bomareoides* A. C. Smith in having its leaves pilose beneath, but differs in having the leaves decidedly bullate, the inflorescence shorter and fewer-flowered, and the flowers smaller in all parts. It is also closely related to *C. duidae* A. C. Smith, the only other *Cavendishia* known from the Pacaraima Mountains, but differs in its bullate leaves which are proportionately broader and its shorter fewer-flowered inflorescences.

Cavendishia caulialata (R. & P.) comb. nov. *Thibaudia caulialata* R. & P. Fl. Peruv. Chil. 4: pl. 386. 1802. *Thibaudia alata* Dun.; DC. Prodr. 7: 562. 1839. *Andromeda alata* Domb. ex Dun.; DC. Prodr. 7: 562. 1839, as syn. *Vaccinium alatum* Domb. ex Dun.; DC. Prodr. 7: 562. 1839, as syn. *Proclesia alata* Kl. Linn. 24: 34. 1851. *Chupalon alatum* Ktze. Rev. Gen. Pl. 2: 384. 1891. *Cavendishia alata* Hoer. Bot. Jahrb. Engl. 42: 279. 1909. In the herbarium of the Museum d'Histoire Naturelle, Paris, there are six sheets collected by Dombey which have been referred to *Thibaudia punctata* R. & P. and *Thibaudia alata* Dun. Of these, four are *Cavendishia punctatifolia* (R. & P.) Hoer. and two are *C. caulialata*, agreeing with the plate of Ruiz and Pavon. These two specimens (one of which, collected at Huasa-Huasi, Department of Junín, Peru, is doubtless the type), differ from *C. punctatifolia* by their shortened inflorescence and short stout campanulate corollas. The broadly winged branchlets readily distinguish the species from other *Cavendishias*. The necessity for the above combination was implied in a recent publication.¹

Cavendishia sophoclesioides sp. nov. Frutex parvus compactus epiphyticus; ramulis cinereis subteretibus juventute parce pallide puberulis mox glabrescentibus; petiolis subrugosis subteretibus decidue puberulis 2–3 mm. longis; laminis crasse coriaceis glabris, subtus dense luteo-glandulosis, ovato-suborbicularibus, 12–15 mm. longis, 8–9 mm. latis, basi apiceque rotundatis, margine integerrimis et crassis, obscure nervatis, costa supra subimpressa subtus elevata, nervis secundariis utroque latere saepe 2, e basi adscendentibus immersis; floribus axillaribus solitariis subsessilibus arcte bracteatis, bracteis

¹ Contr. U. S. Nat. Herb. 28: 312, 509. 1932.

10–20 glabris (margine parce puberulis) oblongo-subspatulatis, maximis et interioribus ad 15 mm. longis et 7 mm. latis; pedicellis circiter 2 mm. longis, bractearum basibus occultis; calyce obconico margine excepto glabro, tubo sub anthesi circiter 2 mm. longo et apice 2.5 mm. diametro, limbo suberecto, lobis inclusis circiter 2.5 mm. longo, lobis deltoideis 1–1.5 mm. longis, basi circiter 2 mm. latis, acutis, margine dense fimbriatis (pilis castaneis, 0.5 mm. longis, basi intercohaerentibus); corolla subcylindrica carnea glabra coccinea (apice lutea?), circiter 20 mm. longa et 4–5 mm. diametro, lobis oblongis, circiter 3 mm. longis et basi 2 mm. latis, subacutis; staminibus subaequalibus circiter 16 mm. longis; filamentis castaneis superne pilos pallidos patulos circiter 0.3 mm. longos gerentibus, alternatim 1.5 mm. et 2.5 mm. longis; antheris alternatim 15 mm. et 14 mm. longis, loculis subgranulatis circiter 3.5 mm. longis, tubulis flexilibus per rimas elongatas dehiscentibus; stylo corollam aequante, stigmate subcapitato.

Type, *Pennell 4354*, collected Feb. 24, 1918, in shrub zone below Páramo de Chaquiro, Western Cordillera, Department of Bolívar, Colombia, alt. 2800–3100 meters, and deposited in the herbarium of the New York Botanical Garden. It is a species very remote from any other known *Cavendishia*, characterized by the solitary subsessile individually bracteate flowers and the small suborbicular leaves. It may be compared in method of inflorescence only to *C. sessiliflora* A. C. Smith, but that species has the inflorescence pubescent, the flowers smaller, the leaves larger and attenuate at base, and many other striking points of difference. The present species has the two staminal series sometimes practically similar.

Satyria polyantha sp. nov. *Polyboea polyantha* Griseb.; Lechl. Berb. Am. Austr. 58. 1857, nomen. *Eurygania polyantha* Benth. & Hook. Gen. Pl. 2: 568. 1876, nomen. *Thibaudia polyantha* Hoer. Bot. Jahrb. Engl. 42: 276. 1909, nomen. *Cavendishia polyantha* Griseb.; Hoer. Bot. Jahrb. Engl. 42: 276. 1909, as synonym. Frutex parvus; ramulis rigidis cinereis teretibus, juventute minute pallide puberulis mox glabrescentibus; petiolis decidue puberulis subrugosis, 4–7 mm. longis, superne anguste alatis; laminis coriaceis elliptico-oblongis, 4–6 cm. longis, 2–2.5 cm. latis, basi cuneatis, apice acutis vel subacutis, margine integerrimis et crassis, supra glabris vel nervis parce puberulis, subtus pilos laxos cinereos circiter 0.5 mm. longos gerentibus, pinnatinerviis, costa et nervis secundariis supra impressis subtus prominentibus, nervis secundariis utroque latere 2 vel 3, arcuato-adscendentibus, jugis inferioribus longissimis, venulis obscure reticulatis; inflorescentiis multis axillaribus 10–25-floris, ubique partibus exterioribus dense et persistenter cinereo-tomentosis (pilis circiter 0.5 mm. longis); rhachide striata 1–3 cm. longa, basi bibracteolata et bracteolis subtenta (bracteolis ovato-oblongis, 2–4 mm. longis, pilis crassis glandulosis circiter 0.2 mm. longis decidue marginatis); calycis tubo campanulato 1.5–2 mm. longo, sub anthesi 2–2.5 mm. diametro, limbo erecto-

patente, lobis inclusis 1–1.5 mm. longo, lobis 5 breviter deltoideis apiculatis, basi circiter 2 mm. latis; corolla breviter cylindrica (juventute subglobosa), 3.5–5 mm. longa, 2–2.5 mm. diametro, lobis 5 deltoideis minutis; staminibus 10 alternatim circiter 3.5 mm. et 4 mm. longis; filamentis castaneis glabris connatis circiter 1 mm. longis; antheris basi minute setosis, alternatim circiter 2.7 mm. et 3.2 mm. longis, apice dilatatis, per rimas elongatas ovaes dehiscentibus, tubulis quam loculis paullo longioribus; stylo crasso quam corolla brevior, stigmate truncato.

Type, *W. Lechler 2068*, collected in June, 1854, at Tabina, Department of Puño, Peru, and deposited in the herbarium of the Royal Botanic Gardens, Kew. Duplicates at Bo, P. Other collections, also from the Department of Puño, are: Between Ollachea and Tabina, *Raimondi 9650* (B); Between Sandia and El Valle Grande, *Raimondi 8996* (B). According to the latter collector, the plant is locally known as “Huihuito” and the fruit is edible. This species forms with its only close ally, *S. neglecta* A. C. Smith of Bolivia, a very distinct group. It is readily distinguished from *S. neglecta* by its pubescent inflorescence, its broader leaves pilose beneath, and by other obvious characters of foliage and inflorescence.

Satyria cerander (Dun.) comb. nov. *Thibaudia cerander* Dun.; DC. Prodr. 7: 565. 1839. The type of this species, which was inadequately described by Dunal, was probably collected in French Guiana by Leblond. Examination of the type collection establishes the fact that it is a *Satyria*, closely related to *S. panurensis* (Benth.) B. & H., from which it differs by its shorter more slender inflorescence and shorter flaring corollas. The corollas apparently never exceed 10 mm. in length, while those of *S. panurensis* at maturity are rarely as short as 16 mm. The presence of a species of the tribe *Thibaudieae* in French Guiana is noteworthy; previously the mountains of British Guiana have been considered the eastern limit of the tribe. The following description is based upon the cited collections:

Glabrous shrub; branchlets subterete, fuscous or cinereous; petioles rugose, 3–5 mm. long; leaf blades coriaceous, ovate-oblong, 7–12 cm. long, 3–5 cm. broad, rounded at base, acuminate at apex, entire at margins, somewhat nitid, 5-plexi-nerved, the costa nearly plane above, prominent beneath, the secondary nerves oriented near base, plane or slightly raised above, raised beneath, the veinlets copiously reticulate, nearly plane; inflorescence axillary, racemose, 4–7-flowered; rachis terete, slender, 6–15 mm. long; pedicels subrugose, 7–12 mm. long, subtended by minute deciduous bracts and minutely bibracteolate near middle; calyx tube campanulate, about 1.5 mm. long and in diameter at anthesis, the limb spreading, 1–1.3 mm. long including the short apiculate lobes; corolla thin-carnose, 8–10 mm. long, 2 mm. in diameter near

base, flaring to about 3.5 mm. in diameter at apex, the lobes erect, deltoid, subacute, about 1 mm. long and 2 mm. broad; stamens about 5 mm. and 6 mm. long respectively; filaments castaneous, glabrous, 1.5–2 mm. long, produced into ligulate connectives; anthers about 4.5 and 5.5 mm. long respectively, slender at base, flaring distally, opening by broad oval clefts about 2 mm. long; style exerted at maturity, the stigma truncate.

FRENCH GUIANA: *Leblond?* (P, herb. Jussieu no. 7575, type). *Leblond*, in 1792 (P). Maroni, *Mélinon* 138 (P, Y).

NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE

1929-1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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The genetics of *Neurospora*—III.

Pure bred stocks and crossing-over in *N. crassa*

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(WITH PLATE 9 AND SIX TEXT FIGURES)

THE DEVELOPMENT OF PURE BRED STOCKS

The mode of segregation of the sex factors in the ascus of *Neurospora crassa* has been reported in a previous paper (Lindegren 1932b). This work involved a number of generations of inbreeding. The first generation consisted of the eight mycelia grown from the eight ascospores from a single ascus. The second generation was obtained by mating mycelia from two of these spores. The spores from seven asci of this generation were induced to germinate. All mycelia produced in the first two generations resembled the wild-type or *normal* mycelium.

The third generation was obtained by mating the mycelium from a first-generation ascospore with mycelia from second-generation ascospores. Mycelia were grown from 32 of these third-generation asci. Thirty-one of them produced ascospores from which only *normal* mycelia were grown. A single third-generation ascus produced four *normal* and four exceptional mycelia. These mycelia were *tan* as described below.

The sex factors in this exceptional ascus were segregated at the first division in the ascus. The factors for *tan* and *non-tan* were segregated at the second division (Lindegren 1932b, fig. 2, b). A mating was made between a *non-tan* and a *tan* mycelium from this ascus, and the ascospores from 55 asci were dissected and mycelia were grown from them. These mycelia fell into two classes, *tan* and *normal*, but there was a wide range of variation in each class. This shows that modifiers affect both the *tan* character and its *normal* allelomorph. In many asci, *tan* and *normal* were segregated at one division, and at least one modifier was segregated differently causing the two pairs of *normal* mycelia to be different and the two pairs of *tan* mycelia also to differ from each other. But members of each pair were always identical. This marked similarity of the two members of each pair is true of all the 55 asci in the f_1 generation.¹ It has also been found in all the many hundred asci from the spores of which the writer has grown mycelia. This proves that the third division in the ascus is equational. Of the 55 asci obtained from the f_1 generation, 48 contained

¹ I am using the symbol f_1 here to refer to the haploid vegetative mycelium developed from ascospores which are cut out after reduction. Strictly speaking, in case of these ascomycetes, the F_1 generation would consist merely of the diploid ascogenous hyphae and the young asci.

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four *tan* and four *normal* mycelia. It is possible that extreme modification of the *tan* gene prevented classification of the other seven asci. Both first- and second-division segregations of *tan* from its *normal* allelomorph were found to occur in the same perithecium.

Descriptions of the pure bred stocks

Black (B). On all media, the *black* mycelia produce a heavy growth of bright orange conidia. On concentrated corn-meal agar, the upper surface of the substrate becomes black. This does not occur on dilute corn-meal agar. *Black*, therefore, resembles the Mendelian character, abnormal abdomen (Morgan 1915), in being markedly dependent on both environment and genetic constitution. It is impossible to change a genetically *non-black* strain to *black* by transfer to richer medium.

Pale (P). Mycelia with the *pale* factor always produce lighter colored conidia than the *black* stock. The substrate in the *pale* cultures darkens on rich media, just as the substrate in the *black* cultures.

Even (E). The aerial hyphae form an even, velvety, orange growth.

Fluffy (F) and *albinistic* (A). These mycelia are very similar. The aerial growth is white, and no conidia, or only a very few, are produced. The *fluffy* mycelia produce numerous small sclerotoid bodies which are not so abundant in the *albinistic* mycelia.

Normal (n). *Normal* cultures resemble the wild-type fungus from which these stocks were developed. The inbred *normal* mycelia are extremely uniform. The f_1 generation *normal* (n) mycelia varied widely from each other.

Tan (T). These cultures are characterized by the development of a tan color in the substrate and few conidia.

Breeding experiments to build up pure bred stocks

A family tree (fig. 1) shows the various matings by which the pure bred stocks were built up. The numbers indicate the serial numbers of the respective asci. The arrangement of the ascospores in the ascus is shown by the four symbols, one for each pair of ascospores. In some cases asci were not dissected. This is indicated by "random." A dash indicates that the mycelium from neither one of the respective pair of ascospores was examined. Each horizontal line constitutes a sexual generation. The first ascus (114) is the progenitor for all the asci shown in the second row.

Black. This stock reproduced itself with perfect fidelity in every one of the seven generations.

Pale. A mating was made between two dark *normal* mycelia of the second generation. Two third-generation asci, resulting from this mating

were dissected. They contained two *normal*, two *tan*, and four *pale* ascospores. Sixty-five third-generation ascospores were selected at random.

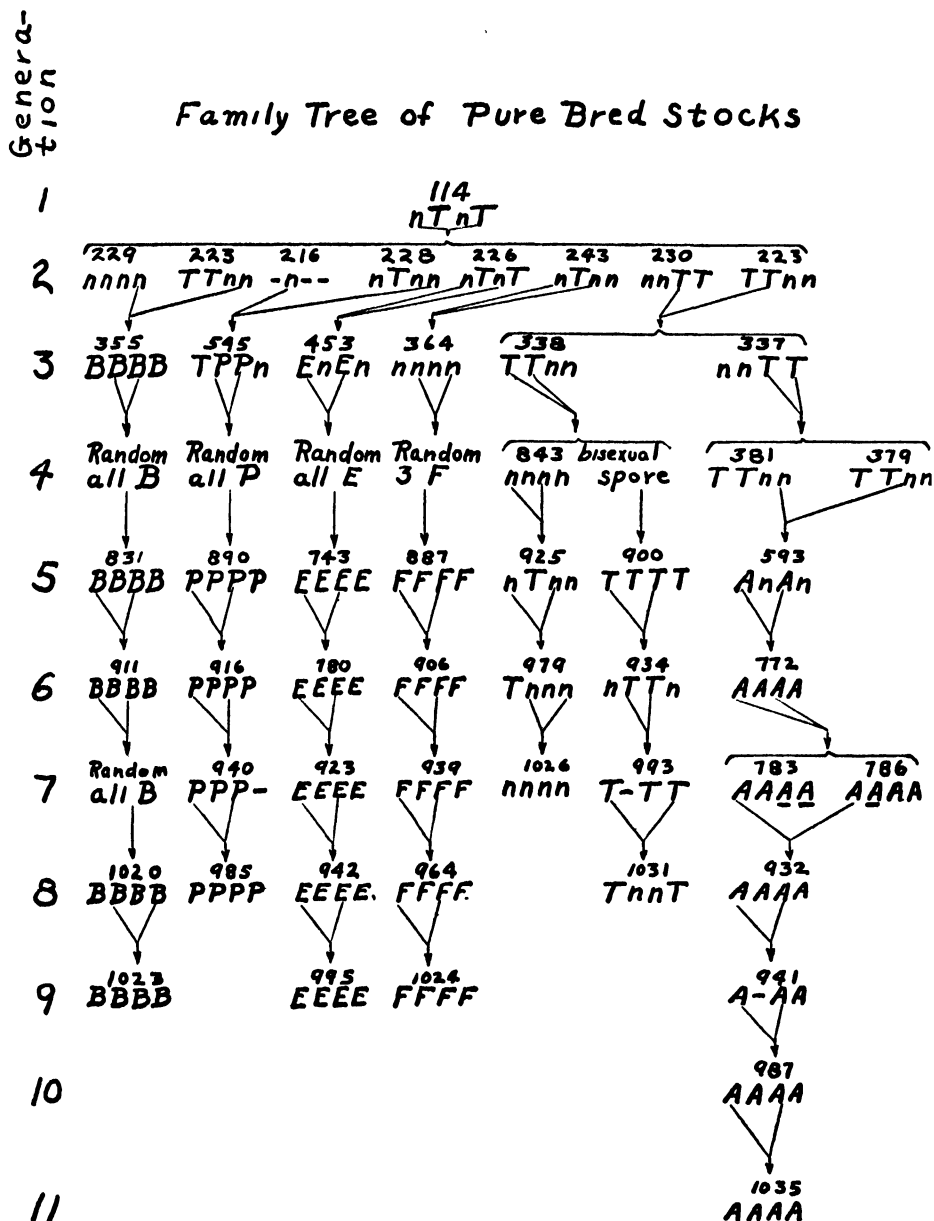


Fig. 1

The mycelia produced by them confirmed this ratio. Mating two of the *pale* mycelia produced only *pale* offspring for the next five generations.

Even. Two *normal* mycelia from ascus 226 were mated. Six of the asci that resulted from this mating were analyzed. They all contained four *even* and four *normal* ascospores. Two *even* mycelia from one of these asci were mated. Only *even* offspring were obtained for six succeeding generations.

Fluffy. Two *normal* ascospores from ascus 243 were mated. Fourteen third-generation asci, resulting from this mating, were analyzed. They produced only *normal* offspring. A mating was made between two mycelia from one of these asci. Thirty-seven ascospores were selected at random. Seventeen produced *pale*, 17 produced *normal*, and 3 produced *fluffy* mycelia, two of these *fluffy* mycelia were mated and only *fluffy* offspring were obtained in four succeeding generations.

The *black*, *pale*, *even*, and *fluffy* stocks all reproduced only their own types in succeeding generations. In this respect they differ markedly from the *tan* stock. On mating two *tan* mycelia, *normal* progeny were always obtained even after seven generations of inbreeding. In general, *tan* by *tan* matings produce half *tan* and half *normal* mycelia. Stocks of the *normal* mycelia produced from these *tan* parents have been built up. They reproduce their own kind in succeeding generations. It has not been possible to build up a pure bred stock of *tan* which produces only *tan* progeny.

Normal. An extensive series of experiments was performed in an attempt to produce a pure bred stock of *tan*. The results threw considerable light on the nature of the inheritance of the *tan* factor and its allelomorph. On mating two *tan* mycelia, *normal* progeny were produced. Although the *normal* and *black* cultures resemble each other closely, the substrate of the *normal* mycelia does not darken on any medium. A short sketch of the development of the *tan* and *normal* stocks will be given using the data in the family tree.

Tan mycelia from asci 230 and 223 were mated. Most of the asci dissected from this mating contained four *tan* and four *normal* ascospores. From ascus 338, two of the *tan* mycelia were again mated. In spite of the fact that both parents and grandparents were *tan*, some of the asci contained all *normal* ascospores. Two *normal* mycelia from one of these asci were mated. A fifth generation was produced, from which three asci were dissected. One ascus contained only *normal* ascospores. Two asci contained six *normal* and two *tan* ascospores.

A mating was made between two of the *normal* mycelia from this fifth generation (ascus 925). Four asci were dissected. Two asci contained only *normal* ascospores. Two asci contained two *tan* and six *normal* ascospores. Two of these *normal* ascospores were mated. Five asci dissected from this mating produced only *normal* mycelia.

Tan. One of the asci produced by mating the two *tan* mycelia from as-

TABLE I
Description of asci analyzed in the inbreeding of the black, pale, even, and fluffy stocks

GENE- ATION	BLACK			PALE			EVEN			FLUFFY		
	NO. ANALYZED ASCI	CHARACTER		NO. ANALYZED ASCI	SPORES	CHARACTER	NO. ANALYZED ASCI	SPORES	CHARACTER	NO. ANALYZED ASCI	SPORES	CHARACTER
3	18	BBBB		2	65	TPPn 17T:17n: 31P	6		EnEn	14		nnnn
4			15		25	all P		150	all E		37	17n:17P: Clon 3F
5	4	BBBB all B	15	2		PPPP	3		EEEE	10		FFFF
6	5	BBBB		4		PPPP	4		EEEE	6		FFFF
7			10	2		PPP-	3		EEEE	1		FFFF
8	4	BBBB		6		PPPP	2		EEEE	5		FFFF
9	3	BBBB					4		EEEE	2		FFFF

cus 338 contained four bisexual ascospores. This is the only case in which any bisexual ascospores have been found in *N. crassa*. The perithecia from each of these bisexual ascospores all contained only the ordinary eight-spored *N. crassa* asci. Most of these asci contained four *tan* and four *normal* ascospores. But one of the asci contained only *tan* ascospores. Two of the *tan* mycelia, from this ascus, were mated. Two of the asci thus produced were dissected. They both contained four *tan* and four *normal* ascospores.

Two of the *tan* mycelia from ascus 934 were mated. Four asci were dissected. These asci had been mutilated so that no more than six ascospores were obtained from a single ascus. Two asci contained both *normal* and *tan* ascospores. In one ascus, 993, all six ascospores were *tan*. Two of these were mated. Four asci were obtained. Each contained four *tan* and four *normal* ascospores.

Albinistic. The *albinistic* stock was developed in the course of an attempt to produce a pure bred stock of *tan*. *Tan* mycelia from asci 223 and 230 were mated. The asci from this mating contained both *tan* and *normal* ascospores. Two of the *tan* mycelia from ascus 337 were mated. Again the progeny were half *tan* and half *normal*. Some of the *normal* mycelia showed a marked tendency to produce non-conidial hyphae. A mating was made between two such *normal*-like mycelia. The asci resulting from this mating contained four *albinistic* and four *normal* ascospores. But there was a third character involved. Some of the *albinistic* cultures had *tan* substrates and reduced aerial mycelium. Some of the *normal* cultures were *tan*. The italic letters *A* and *n* are used for mycelia showing the *tan* character. Table 3 shows that seven of the asci contained four *normal* and four *albinistic* ascospores, with no evidence of the *tan* character. Thirteen of the asci contained either *A* or *n* types of ascospores. One of the asci contained eight *normal* ascospores.

An ascus that did not contain either an *A* or an *n* ascospore was selected. Two of the *non-tan albinistic* mycelia from this ascus were mated. Table 2 shows that the eight asci examined contained only *albinistic* ascospores. But some of these *albinistic* mycelia developed *tan* substrates (*A*).

Again, one of the asci which did not contain *tan* ascospores was selected. A mating was made between two of the *albinistic* mycelia from this ascus (772). Six asci from this mating were examined. All produced *albinistic* mycelia. Three asci produced no *tan* ascospores. One ascus produced two *tan* and six *non-tan* ascospores. Two produced four *tan* and four *non-tan* mycelia.

For the eighth generation, *albinistic non-tan* mycelia were selected from asci which had also produced *albinistic tan* mycelia. These *non-tan albinistic* mycelia were mated, and five of the resulting asci examined. All con-

tained *non-tan albinistic* ascospores. It was concluded that the stock was now free from the *tan* factor. Three more generations were cultured and no more *tan* mycelia were produced.

The failure to produce a pure bred stock of *tan* was not due to failure to establish a uniform environment. When the other pure bred stocks are reproduced vegetatively, the transplants are invariably exactly like the parent cultures. This is not true of the inbred *tan* stock. The first culture

TABLE 2
Description of the asci analyzed in the inbreeding of the albinistic stock

GENERATION	ANALYZED	CHARACTER
Fifth	21 asci	7 AAnn 6 AAnn ^a 4 AAnn 2 AAnn 1 AAnn 1 nnnn
Sixth	8 asci	4 AAAA 3 AAAA 1 AAAA
Seventh	6 asci	3 AAAA 1 AAAA 2 AAAA
Eighth	5 asci	5 AAAA
Ninth	1 ascus	1 A—AA
Tenth	1 ascus	1 AAAA
Eleventh	4 asci	4 AAAA

* An italicized letter indicates that the particular pair of ascospores showed the *tan* character in addition to the one indicated by the symbol.

made by a polysporous transfer from a *tan* culture usually does not have a *tan* color in the substrate, and produces an abundance of conidia. That is to say, it resembles *normal* very closely. When vegetative transfers are made by means of single conidium cultures, *tan*, *normal*, and intermediate cultures are obtained. *Normal* stocks can be obtained in this manner which do not revert to *tan* again following either polysporous or monosporous transfers. This is an irreversible variation. However, it has not been possible to build up stocks of *tan* by monosporous transfers which did not revert to *normal* on subsequent monosporous or polysporous transfer. This

indicates that the *tan* mycelia are heterokaryotic, containing both *tan* and *normal* nuclei. This heterokaryosis probably arises as the result of a mutation of the gene at the *tan* locus to the *non-tan* allelomorph.

Another example of a variation due to heterokaryosis is the following: One of the two unisexual component clones of a race of *Neurospora tetrasperma* produced only a few conidia and darkened the substrate. The other produced an abundance of conidia and did not darken the substrate. The bisexual thallus contained nuclei of both sexes in a common cytoplasm. It was intermediate in appearance and produced perithecia. Such a bisexual thallus was treated by X-rays and subcultured. All subcultures were of the type with a black substrate and few conidia. They were unisexual. A sufficient number of subcultures was made to indicate rather strongly that the other sex had not survived the treatment with X-rays. Without knowledge of the heterokaryotic constitution of such a bisexual thallus (Dodge 1928), and the nature of the cultural characters of the different sexes, it would have appeared that a mutation had been produced by X-radiation. This variation is not the result of mutation, but of the destruction of one type of nucleus in a heterokaryotic mycelium. It is possible that some of the opinions that have been advanced as to the extreme mutability of fungus genes have arisen from experiments with such heterokaryotic stocks which are readily susceptible to variations in the medium.

In the course of the development of most of these stocks, there has occurred the sudden appearance of a new character following inbreeding. The sudden reduction of variability which has accompanied the continued inbreeding in the case of the *black*, *pale*, *even*, *fluffy*, and *albinistic* stocks, indicates that they were produced by the segregation of preexisting genes into separate lines, rather than by new mutations. The variability of the *normal* mycelia in the second generation has been described. Inbreeding these various *normal* (?) mycelia resulted in the appearance of *black*, *pale*, and *even* mycelia in the third generation. *Black* resembles the dark *normal* cultures of the second generation so closely that it is difficult to call it a new form. *Pale* also resembles the dark *normal* of the second generation. *Even*, however, is decidedly different from any mycelia found in the second generation. It is an entirely new type. But the *normal* (?) mycelia from ascus 226 differed from the other second-generation *normal* mycelia in producing bright orange substrates. The production of *even* and *normal* ascospores by mating two of these mycelia with orange substrates, and the stability of the line from this point on, indicate the segregation of a gene, which modifies *even* to *normal*, from the *even* gene.

Fluffy cultures did not appear until the fourth generation, and, again, as stable segregates after inbreeding two generations of apparently *normal*

parents. This may also indicate that a gene modifying *fluffy* toward *normal* had been segregated from *fluffy*.

Albinistic cultures did not appear until the fifth inbred generation, although the fourth-generation *normal* (?) parents of this stock gave evidence of the presence of the *albinistic* gene. Again, this is an indication of the segregation of modifiers of *albinistic* toward *normal* from the *albinistic* gene, rather than a spontaneous mutation.

The fact that continued inbreeding of the unstable *tan* stock always produces some *normal* mycelia indicates that the *tan* gene mutates with rather high frequency to *normal* or *non-tan*. The resulting *normal* mycelia are stable and very seldom revert to *tan*. Genes modifying *tan* to *normal*, which have been shown to exist, may explain the fact that *normal* by *normal* matings occasionally produced *tan* mycelia. Such modifiers may account for the second-generation asci containing two *tan* and six *normal* and some of those containing eight *normal* ascospores. However, since the *tan* and *non-tan* genes were apparently segregated from each other in asci 381 and 379, the reappearance of *tan* in the progeny of the *normal* mycelia from these asci may be the result of a new mutation of the *normal* allelomorph to *tan*. The original appearance of *tan* in ascus 114 and again in the inbred *albinistic* line gives a total of two mutations from *normal* to *tan*. (However, both of these mutations may not have involved the same locus.) The reverse mutation of *tan* to *normal* occurs with high frequency as is shown by the fact that inbreeding of *tan* for eight generations still produces stable *normal* mycelia. We can conclude that the characteristics of the *black*, *pale*, *even*, *fluffy*, and *albinistic* stock are determined by stable genes, while the characteristics of the *tan* stock are determined by an unstable gene which mutates rapidly to *normal*. However, it is indicated that the *tan* mutation probably involves only a single locus and it therefore follows that the genes in all the other loci of the *tan* stock are stable.

In most studies of variation in fungi, the so-called "mutations" have occurred in clones, and the mycelia were propagated as clones. The variants were often obtained following treatment with poisons or heat. Although this type of treatment is not highly effective in producing point mutations in good genetic material, it is most effective in producing "Dauermodifikationen." It might also destroy or favor one type of nucleus in a heterokaryon. Barnes (1929) described some interesting variations in *Eurotium herbariorum*. These variations were induced by heat-treatment. Strict clonal propagation was not practised. Polysporous transfer of ascospores (sexual spores) and conidia (asexual spores) were made. It was these mixed inocula which were subjected to heat-treatment. The variants differed markedly in their stability. Many tended to revert to normal.

Barnes' data show that the most variable forms produced perithecia and ascospores. But the stable ones did not. He did not call attention to this relation. It seems probable that "Dauermodifikation" and the segregation of mutant types by sexual reproduction were involved in the production of the variants. It would be interesting to know if the ascospores were more resistant to the heat-treatment than the conidia.

Miss Heldmaier (1930) carried on a series of experiments on the effect of changes of environment on the ability of various strains of *Schizophyllum* to form clamp connections. This fungus has the tetrapolar type of sex. An AB strain could be altered so that it could copulate with an aB strain. This was assumed to mean that the AB strain was changed, by "modification" of the B gene, to an Ab strain. But another interpretation may seem more probable since it was not proved that a change had been produced in a "factor," only that its expression had been changed.

The facts that it is possible to establish true breeding forms of *Neurospora crassa* by continued inbreeding, and that both members of each of the four pairs of ascospores are identical (no matter how great the variability of the progeny of a mating may be) are strong arguments for believing that most of the genes of this fungus are stable genes.

CROSSING-OVER IN NEUROSPORA CRASSA

The *pale* race is also genetically *tan*, really the double mutant type *tan pale*, but the character *tan* is masked by the *pale* character. That is, *tan pale* mycelia can not be distinguished by inspection from the simple *non-tan pale* strain which may be obtained by segregation in F₁ from a cross of this double type with the *normal* race. *Fluffy* produces practically no conidia. The aerial mycelium is white in color and fluffy in texture. The substrate is colorless, that is, *non-tan*, and genetic tests have shown that this strain does not carry *tan*. Reciprocal matings of these two races were made, and more than 90 percent of the 880 haploid ascospores, produced in 110 asci, were grown and classified for mycelium characters, and a member of each pair of ascospores was tested for sex. The progeny (disregarding *tan* and sex) fell into the following four classes: *pale*, *fluffy*, *pale fluffy* and *normal*. The production of the wild-type class is proof of the fact that each stable haploid race carries the normal allelomorph of the gene which gives the other its characteristic difference from wild-type. In other words, the *pale* race carries the *non-fluffy* gene, and the *fluffy* race carries the *non-pale* gene. The two mutations are not multiple allelomorphs due to mutations in the same locus, but are due to mutation in two separate loci. Since these races are distinguished by characteristics of haploid mycelia developed from individual ascospores, there is no question of or confusion through

dominance and recessiveness, such as is met with in studies of diploid organisms. Each mutant gene is designated by a symbol which is a capital letter and its normal allelomorph is represented by the corresponding small letter. Therefore, the formula of the haploid *pale* parent is Pf, and the formula of the haploid *fluffy* parent is pF. The zygote (ascus nucleus) formed by mating these two races would contain two genes corresponding to each locus. It would be heterozygous for both *pale* and *fluffy*. Its formula would be P/p, F/f (or P f/p F, if the two are in the same chromosome). Reassortment of these genes in meiosis to form haploid ascospores (containing one gene from each pair) would result in the following classes:

P f p F P F p f
pale non-fluffy, non-pale fluffy, pale fluffy, non-pale non-fluffy.

The first division of table 3 shows the frequency of these four types of ascospores among the 440 pairs of ascospores dissected from the 110 asci of the above cross. It has already been shown (Lindegren 1932b) that only the first two divisions in the ascus are reductional. The third division is

TABLE 3

Combinations in 440 pairs of ascospores, summarized for pale and fluffy, fluffy and sex, pale and sex

COMBINATIONS	TYPE	NO.	%	TYPE	NO.	%	TYPE	NO.	%
Original	Pf	114	51.8	F—	111	51.0	P+	169	77.5
	pF	114		f+	111		p—	169	
New	PF	106	48.2	F+	107	49.0	P—	49	22.5
	pf	106		f—	107		p+	49	

equational² (mitotic) for all genes. The two members of each pair of ascospores (1 and 2, 3 and 4, 5 and 6, 7 and 8) are identical genetically. This gives a maximum of four genotypes for the eight ascospores from any one ascus. This shows that *Neurospora crassa* and *Ascobolus magnificus* have different nuclear mechanisms, and indicates strongly that the zygote nucleus in *Neurospora crassa* is diploid. Proof of the diploidy of the ascus nucleus is as follows: All asci examined contained four *pale* and four *non-pale* ascospores, as well as four *fluffy* and four *non-fluffy* ascospores. Therefore, the ratio of *pale* to *non-pale* and *fluffy* to *non-fluffy* in the total population was 1:1. If the ascus nucleus were tetraploid in *Neurospora crassa*, this ratio could not be obtained without a second meiosis. In the absence of brachymeiosis, a ratio of 1:4:1 would be found (Haldane 1930) in the total population (not from each ascus). The diploid genotypes of this ratio

² Since this division is invariably equational it cannot be a brachymeiosis (Gwynne-Vaughan and Williamson, 1932) in the case of *N. crassa*.

would be, 1 *pale pale*: 4 *pale non-pale*: 1 *non-pale non-pale*, and the same in the case of *fluffy*. This, therefore, is the condition which would obtain if the ascus nucleus were tetraploid and a brachymeiosis did not occur. Since this ratio is not found and brachymeiosis does not exist in *N. crassa*, the other alternative is that the first fusion, said by some to occur at the origin of the perithecium, is followed by a reduction in the crozier or previously. In such a case the two haploid nuclei fusing in the young ascus should be both *pale* in 25 percent of the cases and both *non-pale* in 25 percent of the cases, while only 50 percent of the young asci would be heterozygous for *pale* and *non-pale*. The same reasoning applies in the case of *fluffy* and *non-fluffy*. Since every ascus nucleus was heterozygous for both of these pairs of genes, a perithecial fusion, if such there be, is not followed by a reduction before the formation of the crozier. Therefore, only a single fusion occurs in *N. crassa* and the ascus nucleus is diploid. This diploid nucleus is immediately reduced in the normal way by a meiosis involving only two reduction divisions.

Since the diploid zygote nucleus in the above cross was heterozygous for still another pair of genes, $+-$, the number of possible classes of ascospores was eight, as follows: $Pf+$, $Pf-$, $pF+$, $pF-$, $PF+$, $PF-$, $pf+$, and $pf-$. In the absence of linkage, each of these eight classes should occur in equal numbers in random samples of ascospores. But any one ascus would contain a maximum of four of these types of ascospores, and some would contain only two types.

In the absence of linkage, the four possible classes with respect to *pale* and *fluffy* should occur in statistically equal numbers, and the data show that equality is approximated. The practical equality of the original combination with the recombination classes shows that these two genes are not linked. When four Pf ascospores are present in one ascus, the other four spores are necessarily pF . This accounts for the exact equality of these two types in the above data as well as for the exact equality of the pf and PF classes, for at least one member of each pair of ascospores of each ascus was raised.

The pf ascospores contain the normal allelomorphs of both the *pale* and the *fluffy* genes. The mycelia grown from such ascospores (disregarding *tan*) are identical with the wild-type fungus from which the various mutants were developed. The new double type, *pale fluffy* shows characteristics of both parent types in combination, and is as stable as the parents. It does not form sectors of *pale* or *fluffy*, and, naturally, this would not be expected since both genes have been incorporated into the same nucleus. *Pale fluffy* shows a modification of each of the original types since they now are acting together on the same features of the mycelium.

Each mutant gene was segregated from its normal allelomorph at the first division in some asci and at the second division in other asci. This can be readily deduced from the seriation of the characters in the eight ascospores after they have been raised and classified. Table 4 gives the data on the frequencies of first- and second-division segregation for + versus -, *pale* versus *non-pale* and *fluffy* versus *non-fluffy*. The data on segregation of the sex factors contain additions from crosses other than the one under consideration, while the P/p summary lacks one of the 110 asci.

It has been shown (Lindgren 1932b) that the ratio of first- to second-division segregation of the sex factors is a constant, namely, 87.1:12.9 (corrected by new data). The data in table 4 on the segregation of p from P and f from F show that, in these cases, the ratios are different from that

TABLE 4

Distance from spindle fiber of locus for sex, for pale and for fluffy, deduced from percentage of asci showing second-division segregation

DIVISION	+/-	%	P/p	%	F/f	%
I	391	87.1	73	67.0	42	38.2
II	58	12.9	36	33.0	68	61.8
Distance	6.5		16.5		30.9	

for the sex factors and apparently are specific for each pair of allelomorphs. A consistent explanation, following a suggestion for which the writer is indebted to Dr. E. G. Anderson, can be built up on the basis of the following two assumptions: (1) Crossing-over occurs at the four-strand stage. (2) The spindle-fiber attachment is always segregated reductionally at the first meiotic division (the first division in the ascus). It follows that the percentage of second-division segregation is a measure of the distance of a gene from its spindle-fiber attachment. Second-division segregation of a gene pair would result from single crossing-over of two homologous strands at the four-strand stage between the spindle-fiber attachment and the locus of the gene. This is shown in figure 2. A proof that these two assumptions are true can be obtained by comparing map distances calculated by the ordinary means without reference to the ratio of first- to second-division segregation with map distances calculated from the ratio of first- to second-division segregation. The same data may be used for this comparison since these two methods are entirely independent. This can be seen by arbitrarily rearranging the spores shown in the asci in table 7. For example, all the asci in class 2 could be changed into class 3 as follows:

$P + P - p - p +$ (PI; +II) could be changed to $P + p + P - p -$ (P II; +I). But any amount of change of this nature would not alter the linkage of *pale* to sex of 22.5 which is shown in table 1. These assumptions then will be demonstrated to be true if the map distance calculated by means of the ratio of first-division to second-division segregation is statistically equivalent to 22.5. As a result of the second divisions each ascus in which such single crossing-over has occurred contains two crossover and two non-crossover chromatids, and, as the result of the third or purely equational

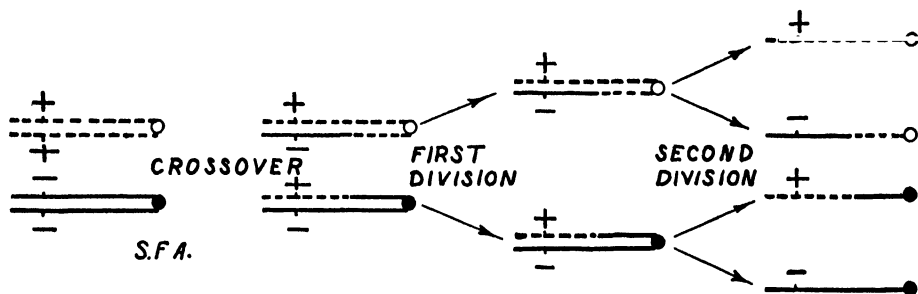


Fig. 2. A diagram to show how single crossing-over between the spindle-fiber attachment (s.f.a.) and the locus of sex (+, -) results in second-division segregation of (+) from (-). At the left, the paired chromosomes are shown at the four-strand stage. Next, the arrangement following crossing-over is shown. The spindle-fiber attachments separate reductionally at the first meiotic division, carrying a + - combination into each of the first two nuclei. At the second-division the spindle-fiber attachments divide equationally, producing the four-nucleate stage, with the nuclei arranged in the ascus in the order in which they are shown in the diagram. Different random orientations of either or both dyads at the binucleate stage would produce other typical second-division segregation configurations. The third (mitotic) division does not change the configuration. The first chromatid corresponds to the first pair of identical ascospores, the second chromatid to the second pair of ascospores, etc.

divisions, four crossover and four non-crossover ascospores. Only half of the pairs of ascospores produced after each second-division segregation contain crossover chromatids. Where all of the ascospores are grown, each case of single crossing-over between the spindle fiber and the locus can be detected. In such diploid organisms as *Drosophila*, one chromatid from each four is sampled and hence in half the reductions in which single crossing-over has occurred, the sample shows a non-crossover chromatid. To express the distance between the spindle-fiber attachment and the locus of a gene in standard crossover units, the percentage of second-division segregation asci is merely divided by 2. This is a method of obtaining certain map distances without dependence on the four class associations of two pairs of linked genes. By this method the distances from the spindle-fiber attachments of the genes for *pale*, *fluffy* and sex were determined, and are

given in the last line of table 4. These values are really "recombination percentages" for the spindle fiber and the gene whose percentage of second-division segregation is being studied. If two cases of crossing-over occurred between this locus and the spindle fiber, the gene would segregate at the first division instead of at the second. Hence, as in the general situation in *Drosophila* and elsewhere, the recombination percentages can be used as map distance only when the distance between the two loci is short enough so that double crossing-over within is negligibly rare. In the case of recombination percentages deduced from second-division segregation, any kind of double within the interval will result in a discrepancy between the recombination percentage and the map-distance. A recurrent double, a progressive double or two independent singles in this interval will cause two crossovers to fail to register as recombinations.

Table 5 shows that with respect to the segregation of the two pairs of genes, P/p and F/f, four classes of asci were found. In class 1, for example, the mutant and the normal genes for both pairs were segregated from each

TABLE 5
Classes of segregation with respect to pale and fluffy, deduced from serialations of pairs of ascospores in 110 asci

CLASS	DIVISION	SUBCLASSES				NO. ASCI	%	CALCULATED %
		1 & 2	3 & 4	5 & 6	7 & 8			
1	P/p I	PF	PF	pf	pf	13	26.3	25.6
	F/f I	Pf	Pf	pF	pF	16		
2	P/p I	PF	Pf	pf	pF	10	40.9	41.4
	F/f II	PF	Pf	pF	pf	15		
		Pf	PF	pf	pF	7		
		Pf	PF	pF	pf	13		
3	P/p II	PF	pF	Pf	pf	5	12.7	12.6
	F/f I	PF	pF	pf	Pf	5		
		pF	PF	pf	Pf	2		
		pF	PF	pf	Pf	2		
4	P/p II	pf	PF	PF	pf	1	20.0	20.4
		PF	pf	pf	PF	1		
		PF	pf	PF	pf	4		
	F/f II	PF	pf	Pf	pF	2		
		Pf	pF	PF	pf	3		
		PF	pf	pF	Pf	2		
		pF	Pf	PF	pf	2		
		pF	Pf	pF	Pf	2		
		pF	Pf	Pf	pF	3		
		Pf	pF	pF	Pf	2		

other at the first division. Each of the four classes contains subclasses, shown in this table, where the end to end seriation in the ascus is disregarded. In the absence of linkage, each of the two subclasses in class 1 should be present in statistically equal numbers. If the genes were linked, the Pf Pf pF pF original combination asci should be more numerous than the pf pf PF PF recombination asci. Sixteen original combination and 13 recombination asci were found. This approximate equality proves that the genes in question are not linked.

Table 6 shows the classification of 109 asci with regard to *fluffy* and *non-fluffy*, as well as + and - sex. The linkage relations already discussed (table 3) indicate that these genes are not linked. In table 6 the approximate equality of the two subclasses (20 and 16) in class 1 confirms this view.

TABLE 6

Classes of segregation with respect to fluffy and sex deduced from the seriations of pairs of ascospores in 109 asci

CLASS	DIVISION	SUBCLASSES				NO. ASCI	%	CALCULATED %
		1 & 2	3 & 4	5 & 6	7 & 8			
1	F/f I	F-	F-	f+	f+	20	33.0	33.3
	+/- I	F+	F+	f-	f-	16		
2	F/f I +/- II	F+	F-	f-	f+	1	5.5	4.9
		F-	F+	f+	f-	1		
		F+	F-	f+	f-	1		
		F-	F+	f-	f+	3		
3	F/f II +/- I	F+	f+	f-	F-	14	55.0	53.8
		f+	F+	F-	f-	19		
		F+	f+	F-	f-	13		
		f+	F+	f-	F-	14		
4	F/f II +/- II	F+	f-	f-	F+	2	6.5	7.9
		F+	f-	F+	f-	1		
		F-	f+	F+	f-	2		
		f+	F-	f-	F+	1		
		F-	f+	F-	f+	1		

In table 7, the asci are classified with regard to *pale* and sex, (+) and (-). Correction has been made for reciprocal crosses by reversing the signs for sex in one of the matings. The parental classes are P (+) and p (-). The recombination classes are P (-) and p (+). Sixty-two P(+) P(+) p(-) p(-) asci were found in class 1 and only one P(-) P(-) p(+) p(+) ascus. Therefore, *pale* is strongly linked to the sex-differenti-

ators. We may call the chromosome containing the sex differentiator the sex chromosome, and call *pale* a sex-linked gene. The distance of *pale* from the spindle-fiber attachment is 16.5 (plus an unknown amount due to unobserved doubles). The distance of (+) from the spindle-fiber attachment is 6.5. Here the distance is so short that the correction for unobserved doubles may be very slight. It follows that the distance between (+) and *pale* is either approximately 23.0 ($16.5 + 6.5 = 23.0$) or approximately 10.0 ($16.5 - 6.5 = 10.0$). These are the two possible solutions obtained from data on the percentage of second-division segregation. They are determined in-

TABLE 7

Classes of segregation with respect to sex and pale as deduced from the seriations of pairs of ascospores in 109 asci

CLASS	DIVISION	1 & 2	3 & 4	5 & 6	7 & 8	NO. ASCI		%	CALCULATED %
1	P/p I	P+	P+	p-	p-	62			
	+/- I	P-	P-	p+	p+	1	63	57.8	58.3
2	P/p I	P+	P-	p-	p+	3			
	+/- II	P+	P-	p+	p-	1	10	9.2	8.6
		P-	P+	p-	p+	3			
		P-	P+	p+	p-	3			
3	P/p II	P+	p+	P-	p-	8			
	+/- I	P+	p+	p-	P-	9			
		p+	P+	P-	p-	7	34	31.2	28.7
		p+	P+	p-	P-	10			
4	P/p II	P+	p-	p+	P-	1			
	+/- II	p+	P-	P-	p+	1	2	1.8	4.3

dependently of the association of *pale* and sex observed in the mycelia developed from the ascospores. Table 3 contains the linkage data. The observed recombination percentage for sex and *pale* is 22.5. This agreement with the expectation of 23.0 proves the validity of the assumptions upon which the calculations of the map distance from the segregation data were based. Therefore, it has been demonstrated that (1) crossing-over occurs in the four-strand stage, and (2) the spindle-fiber attachment is segregated reductionally at the first meiotic division. It is interesting to note the high similarity between the meiotic mechanism in this organism and that in such an organism as *Drosophila*. *N. crassa* is superior in that all the products of each reduction can be accurately known instead of having to be deduced from the sample of one chromatid from each reduction, or two chromatids in the more favorable cases of non-disjunction, attached-Xs, or triploid studies.

Figure 3 is a map of the sex-chromosome, based on the data thus far accumulated, but uncorrected for double crossing-over. Asci in class 2 (table 7) are produced by a single crossover in the (+) arm, which we may call the "left" arm. Asci in class 3 are produced by a single crossover in the



Fig. 3. Map of the sex chromosome of *Neurospora crassa*.

pale or "right" arm. Figure 4 is a diagram showing how this crossing-over would produce asci falling into class 3. The orientation of the chromatids has been given for only a single possibility.

Irrespective of whether genes are linked or independent, it is possible to calculate the percentages of asci falling into each of the four classes by the known percentages of first- and second-division segregation (table 4). The product of the percentage of first-division segregation of P from p (expressed as a fraction) by the percentage of first-division segregation of

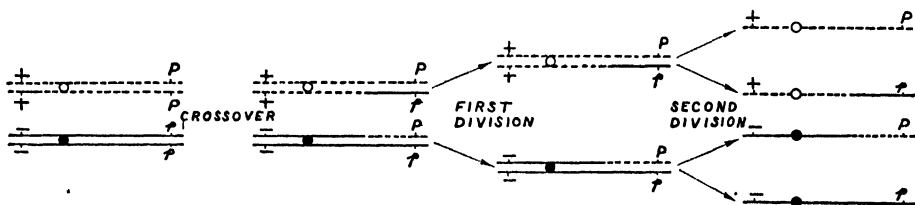


Fig. 4. A diagram to show how crossing-over between the locus of *pale* (P) and the spindle-fiber attachment (s.f.a.) produces asci of class 3 (table 7). The two homologous chromosomes are shown at the four-strand stage. The first division is reductional with regard to (+) and (-) and equational with regard to (p) and (P). Changes of orientation produce the four sub-classes found in class 3, table 7.

F from f ($.670 \times .382 = .256$) gives the percentage of asci in which both pairs of genes are segregated at the first division, and similarly for the second-division expectation, etc. This has been done in tables 5 and 6 for the independent combinations. In the case of independent genes, the calculation merely involves the assumption that crossing-over in one chromosome has no effect on crossing-over in another chromosome. Although this assumption may not be generally true (Redfield and Schultz in Morgan, Bridges and Schultz 1930), the agreement between the calculated and the observed percentages for these cases indicates that it is correct for the regions involved here.

In table 7 this calculation has also been made. It is important to observe that in the case of linked genes, this calculation involves a different

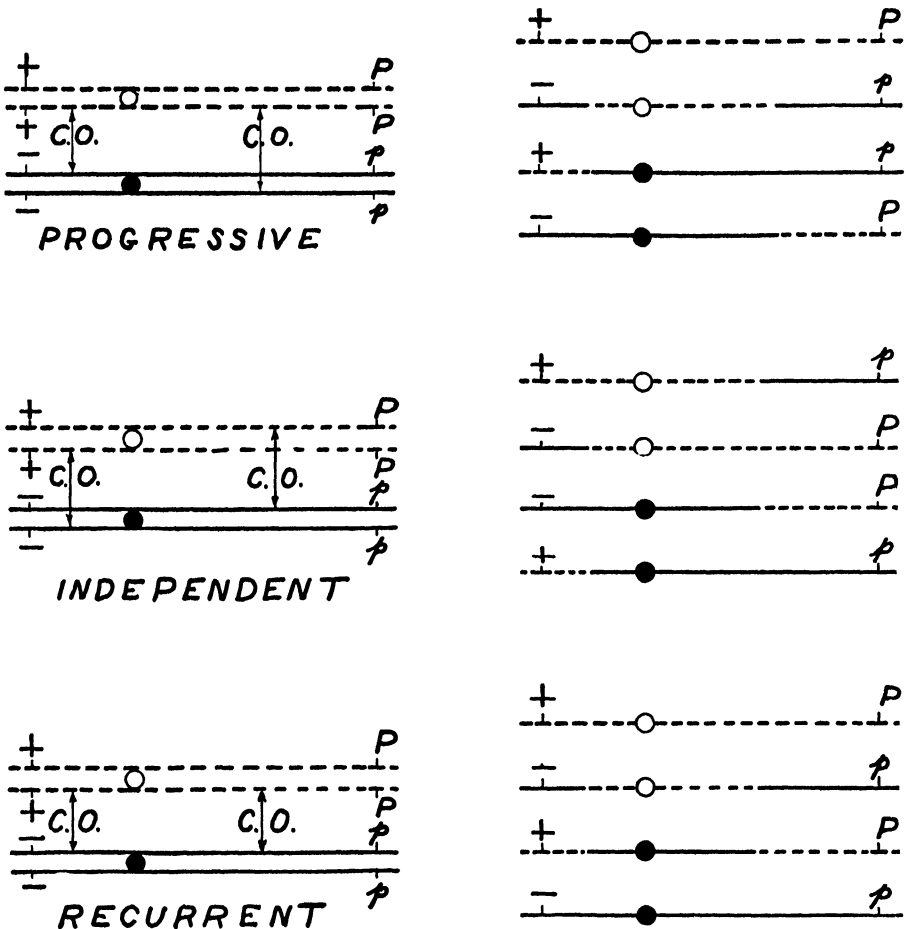


Fig. 5. A diagram showing the configurations of ascospores in the ascus which would result from progressive, independent, and recurrent compound crossovers. The double headed arrows, marked c.o., show the points at which the crossovers occur and the strands involved.

In the diagram of the progressive compound crossover, the upper chromatid at the right ($P+$) (corresponding to ascospores 1 and 2) is a non-crossover. The second chromatid, ($p-$) (corresponding to ascospores 3 and 4) is a double crossover. The third chromatid ($p+$) (corresponding to ascospores 5 and 6) is produced by a single crossover between $+$ and s.f.a. The fourth chromatid ($P-$) (corresponding to ascospores 7 and 8) is produced by a single crossover between p and s.f.a.

The diagram of the independent compound crossover follows the same scheme. This type is called independent because two different pairs of non-homologous strands cross over with each other. Four single crossover chromatids are produced. In such an ascus, complete reversal of linkage occurs.

In recurrent compound crossover asci, two double crossover and two non-crossover chromatids are produced. The name 'recurrent' is used because the same two non-homologous strands are involved.

viewpoint. In the case of the sex chromosome, the calculation is based on the assumption that a crossover in one region of this chromosome does not interfere with a second crossover in an adjacent region, but that crossovers are distributed at random, without "interference." Since the two regions are on opposite sides of the spindle-fiber attachment, this may very well be true, even for loci close together. The agreement in the case of the linked genes is not so close as in the case of the independent genes, but the numbers are too small to be significant as to the presence of an interference effect.

The asci found in class 4 and the recombination ascus in class 1 are produced by two crossovers in the sex chromosome. Those in class 4 will be designated compound-crossover asci to distinguish them from double-crossover chromatids. These compound-crossover asci can be divided into three main groups, called progressive, independent and recurrent. One progressive and one independent were found. The progressives contain one double-crossover chromatid, one non-crossover chromatid, and two single-crossover chromatids. The independents contain four single-crossover chromatids. The recurrents (none was found) contain two double-crossover chromatids and two non-crossover chromatids. The calculation of the expected percentage of compound-crossover asci, on the assumption of random distribution of crossing-over, is made by taking the product of the fractions representing second-division segregation (not the fraction representing the amount of crossing-over) for each region involved. For example, $.330 \times .129 = .0426$. As already stated, the numbers are too small to permit conclusions regarding the significance of an interference effect. The calculation of the expected percentage of double-crossover chromatids is made according to the method commonly used by taking the product of the fractions representing the two adjacent map distances. For example, $.065 \times .165 = .0107$. Let us say that roughly 4 percent of compound-crossover asci (segregation method) and 1 percent of double-crossover chromatids (linkage method) are calculated. Then, to take a concrete example, 4 asci in every 100 asci should be compound-crossover asci. One hundred asci contain 400 chromatids. Therefore, 1 percent, or 4 chromatids out of 400 chromatids, should be double-crossover chromatids. If the two methods of calculation (segregation and linkage) are in agreement, four compound-crossover asci should, on the average, contain four double-crossover chromatids. It is planned to test this point with larger numbers.

The recombination ascus in class 1 (table 7) is capable of two explanations (fig. 6). It could result from two simultaneous independent-crossovers between *pale* and the spindle-fiber attachment, or by two simultaneous independent-crossovers between (+) and the spindle-fiber attachment.

The *pale* parent used in the above cross was genetically *tan* as well. In the progeny the *fluffy* (pF) mycelia could be classified into two groups: *fluffy tan* (pFT) and *fluffy non-tan* (pFt). The *non-pale non-fluffy* (pf) progeny could also be classified with respect to *tan*. Both *tan* (pfT) and *non-tan*

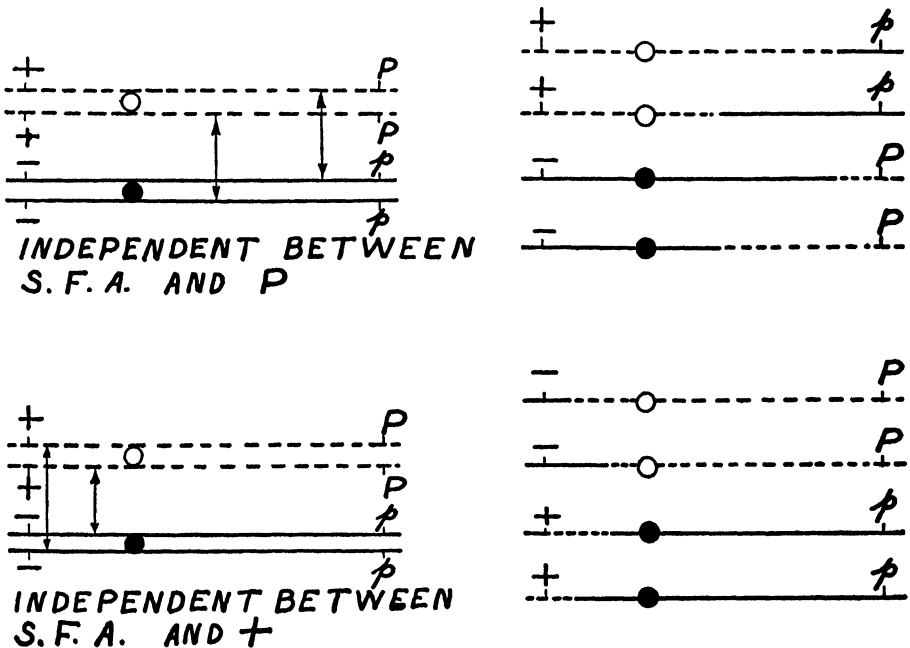


Fig. 6. A diagram showing two possible explanations of the recombination ascus in class 1 (table 7).

(pft) were found. In both cases, the *tan* and *non-tan* classes occurred in equal numbers. This proves that *tan* is not linked to either *pale* or *fluffy*. *Pale* and *pale fluffy* mycelia could not be classified into *tan* and *non-tan*.

SUMMARY

The development of six stable pure bred stocks and one constantly mutating stock is described. It is suggested that the stable stocks were produced by the segregation of modifying genes from the genes differentiating the stocks. The stability of these six stocks, and the fact that the constant mutation is apparently at a single locus, suggest that most of the genes in this fungus are stable. It is suggested that many of the apparent mutations in fungi may be due to "Dauermodifikationen" and the selection or destruction of one nucleus in a heterokaryon, rather than to "point mutations."

Evidence is offered indicating (1) that the ascus nucleus in *Neurospora*

crassa is diploid; (2) that the reduction of the diploid nucleus to four haploid nuclei is effected in the first two divisions of the ascus nucleus; (3) that crossing-over occurs at the four-strand stage; (4) that the spindle-fiber attachment is segregated reductionally at the first meiotic division.

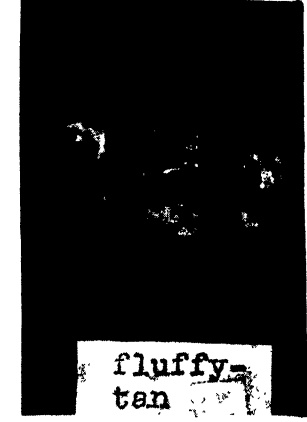
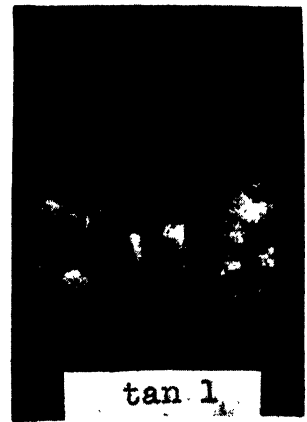
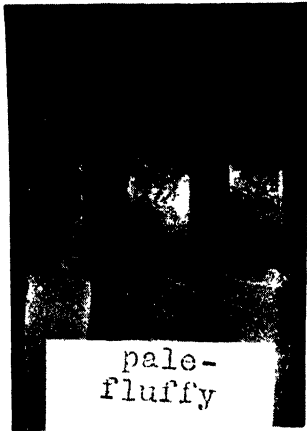
A three-point map of the sex chromosome is constructed, and the types of crossing-over in the two adjacent regions are discussed.

The writer is grateful to Dr. T. H. Morgan for his continued interest. He has enjoyed the privilege of discussing the problem with Dr. Albert Tyler, Dr. E. G. Anderson, Dr. Calvin B. Bridges, Dr. S. H. Emerson, and Dr. A. H. Sturtevant. He is particularly indebted to Dr. Bridges for his helpful revision of the manuscript, and to Dr. B. O. Dodge for editorial criticism.

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Autogamous Turkestan rye

BASIL M. BENSIN¹

(WITH THREE TEXT FIGURES)

This new species of rye was discovered by the writer in 1912, while engaged in an expedition organized by the Russian Bureau of Applied Botany for the investigation of Turkestan cereals, chiefly in their relation to drought-resistance. It was found in cultivation in the field of a Kirghizian farmer by the name of Dair Barzabaeff, about ten miles from Aulie-Ata, in Syrdaria Government.

According to native Kirghizians, this type of rye appeared in comparatively recent times mixed with the wheat, gradually becoming a dominant plant in the wheat-fields. The local Kirghizian name for it is Kara-bidaj ("black wheat"), and they supposed that their white wheat (Ak-bidaj) gradually degenerated into black wheat (Kara-bidaj), not realizing that the plant was actually rye. It was sold in the market at Aulie-Ata, in 1912, at the same price as wheat: 1 ruble per pood or about \$1.00 per bushel.

The local wheat consists entirely of early varieties: white wheat (*Triticum vulgare* var. *graecum* Körn.) in very many forms, and durum wheat (*Triticum durum* var. *hordeiforme* Host). Both of these species have light-colored kernels, white or yellow, so the dark brown kernels of the new species of rye were quite conspicuous in the lots of grain.

The rye is thus replacing the wheat as a crop plant, apparently because it is better adapted to the local climatic and cultural conditions (agrorchora). We have here a case of competition, in cultivation, between two crops, the better-fitted becoming dominant. The yield of the rye, however, was not very high; it was said to amount to about 50 poods per desiatin (12.3 of a bushel per acre) on irrigated land. Only locally home-made plows are in use.

The author described this Turkestan rye in a report on his Turkestan trip, published in the Bulletin of the Bureau of Applied Botany in 1913, with illustrations but without a formal name or Latin diagnosis.² On the basis of morphological characters and geographic distribution he regards

¹ The author wishes to thank Dr. H. A. Gleason and Dr. J. H. Barnhart of The New York Botanical Garden for the encouragement and kind assistance in preparation of this article and to Dr. E. D. Merrill who made it possible to publish it.

² Benzin, B. M. The notes on my Turkestan trip. Bull. Angew. Bot. 1913: 459-495. 1913. (Russian, with English résumé. Reprinted in Russian, with slight alterations and a changed title, Tashkent, 1915.)

it as a distinct species, and as an agroecological xerophytic chorotype, and accordingly here supplies it with both name and diagnosis:

Secale turkestanicum Bensin, sp. nov., spiculis semper trifloris, floribus omnibus aut ullis 2 fertilibus; lemmatibus latis ad basin carinatis; paleis ad lemmata etiam usque ad maturitatem arcte adhaerentibus et floribus ergo autogamis; rachide basi albopiloso rigido nec fragile; granis oblongis basi acute carinatis atro-brunneis aut basi paene nigris firmissime adhaerentibus neque ad maturitatem diffractis. Habitat in valle fluviorum Talas et Chu, cultum, prope Aulie-Ata, Sirdaryatan, Turkestan, Asia centralis.

Turkestan rye has the spikes usually about twice as long as in ordinary cultivated rye; the long rachis very stiff but not fragile, conspicuously villous at the base of each spikelet.

There are always three flowers in each spikelet, which are designated in the accompanying figure as f , f_1 , and f_2 . Sometimes all three bear fruit, but commonly this is true of only two (f and f_1 , f and f_2 , or f_1 and f_2); in the first case, the uppermost flower is smaller. The lemma and palea are so closely appressed to each other that the flower can not open during pollination, so it is evident that this species is self-pollinated (autogamous).

The kernels are more elongate than in ordinary rye, *Secale cereale*, and are much narrower and pointed at the base, where the embryo is situated. They are dark brown above and black below. They are firmly attached at the base, and are so completely covered by the lemma and palea that they are hidden even when fully mature and dry, consequently they do not shatter, as does ordinary rye.

The most essential differences from ordinary rye have been indicated above, but may be here summarized: (a) invariable development of three flowers instead of two in each spikelet; (b) frequent maturity of the fruit of the uppermost flower; (c) complete enclosure of the flower in the lemma and palea, and consequent self-pollination, instead of an open flower with cross-pollination; (d) firm attachment of the kernels and consequent non-shattering upon maturity, instead of easily shattering kernels; (e) stronger development of villous hairs at the base of each spikelet; (f) dark, almost black, color of the kernels.

Agroecological features. This rye chorotype of Turkestan possesses distinctly xerophytic adaptations. The protection of its pollen with the resulting autogamy is a striking adjustment to its climatic environment, which is characterized by dry south-eastern winds. The protection afforded to the spikelet by the villous hairs at its base is another xerophytic character.

The firm attachment of the kernels is also important from an agroeco-



Fig. 1. *Secale turkestanicum* Bensin. Natural size of fully mature ear.

logical standpoint, in a region where agriculture is poorly developed and there is no harvesting machinery except the sickle and the scythe. The crops mature more rapidly than they can be harvested, and the Kirghizians would lose more than three quarters of the yield if they grew ordinary rye, with its strongly shattering kernels.

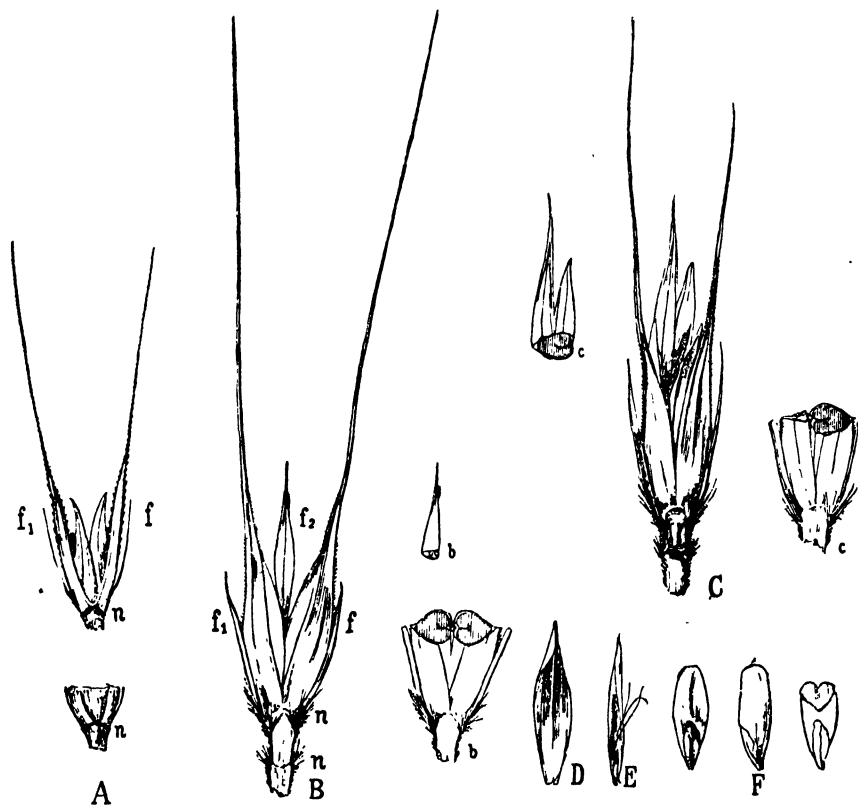


Fig. 2. Comparison of *Secale turkestanicum* with *S. cereale*. A. Spikelet of *Secale cereale* L. f, f₁, two flowers; n, glabrous base of spikelet. B. Spikelet of *Secale turkestanicum* Bensin. f, f₁, f₂, three flowers; n, hairy base of the spikelet; c, section of lower fruiting and one upper flower. C, spikelet with fruiting lower and upper flower. D, palet of fruiting flower. E, palet of unfertilized flower. F, kernel.

Previous records of rye with 3-flowered spikelets. In 1812, Palisot de Beauvois³ named as a new species *Secale triflorum*. All he says about it is: "J'ai trouvé cette dernière espèce à Dunkerque sur les bords d'un nouveau canal qui conduit à la mer. Elle ne diffère du *S. cereale* que par la troisième

³ Palisot de Beauvois, A. M. F. J. Essai d'une nouvelle agrostographie. 1-182. 1812. (*Secale triflorum* on page 105.)

fleurette." It is evident from his generic description that the third flower was sterile.

In 1857, Döll⁴ described a variety of ordinary rye, *Secale cereale* var. *triflorum*, "Aehrchen mit lang gestielter dritten Blüthe," as not rare in wet seasons as solitary specimens in various places in Baden. His generic description, however, shows that the third flower, when present, was rudimentary.

In 1881, Regel⁵ described in few words an Asiatic plant that he regarded merely as a variety of ordinary rye, under the same name, *Secale cereale* var. *triflorum*: "spicula triflora, flore supremo pedicillato masculo. Colitur in Chiwa."

In 1885, Körnicke, discussing⁶ abnormalities of development in rye, devotes nearly half a page to the occurrence of 3-flowered spikelets. He cites Palisot de Beauvois, Döll, and Regel, commenting upon the rarity of specimens with three fertile flowers, and mentions one record of spikelets each of which produced four perfect kernels. These were all, however, in other respects ordinary rye.

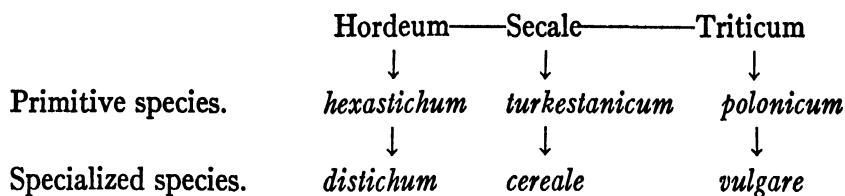
Relation of S. turkestanicum to S. cereale. While *S. turkestanicum* has a local and limited distribution in Turkestan, being an endemic Turkestan plant, it may shed light upon the relationship between *Secale* and other genera of Gramineae, especially the cultivated ones *Hordeum* and *Triticum*. I assume that it is a more primitive species than *S. cereale*, which has probably been derived from it during the centuries since rye was first cultivated in Asia and Europe. It is rougher, with the flowers in the spikelets unevenly developed, but is better adapted to a wild state, where it grows scattered and isolated, and is more resistant to drought, while *S. cereale* is more highly specialized, and is adapted to a milder climate and better cultivated fields.

We might compare *S. turkestanicum* with *Triticum polonicum*, which it resembles, and with *Hordeum hexastichum*, also with three developed flowers. These three would form a series of more primitive species than *S. cereale*, *T. vulgare*, *H. distichum*, as may be graphically illustrated by the following table.

⁴ Döll, J. C. Flora des Grossherzogthums Baden. 1-1429. 1857-62. (*Secale cereale* var. *triflorum* on page 122.)

⁵ Regel, E. A. von. Descriptiones plantarum novarum et minus cognitarum. Fasciculus VIII. Acta Horti Petrop. 7: 541-677. 1881. (*Secale cereale* var. *triflorum* on page 579.)

⁶ Körnicke, F. A. Die Arten und Varietäten des Getreides. (In Körnicke & Werner. Handbuch des Getreidebaues.) 1-470. *pl.* 1-10. 1885. ("Bildungsabweichungen" on pages 119-121.)



Secale turkestanicum thus lessens the gap in the relationship between the genera *Hordeum*, *Secale*, and *Triticum*, which have had such an enormous influence in the history of agriculture and of human culture.



Fig. 3.

Unfortunately, I have no prospect of being able to make further detailed studies and experiments with *S. turkestanicum*, which would be such an interesting subject for plant-breeding work and agroecological investigations in the arid and subtropical regions.

NEW YORK CITY

A review of recent work on the effect of ultraviolet radiation upon seed plants

H. W. POPP AND FLORENCE BROWN¹

INTRODUCTION

Prior to 1927 it had generally been conceded by those who had examined carefully the experimental evidence available, that ultraviolet radiation, particularly the shorter wave lengths, was inimical to higher plants. Since 1927, however, numerous papers have appeared in which an apparent effort has been made to demonstrate beneficial effects on higher plants comparable to those reported as occurring in the animal organism. These beneficial effects as a rule have not been very outstanding. Unfortunately many of the papers report the results of extremely short experiments without adequate controls, carried out with so few plants as to render the conclusions extremely doubtful. In no case has the ultraviolet to which the results have been attributed been the only variable in the test plants as compared with the controls. So long as this is true results obtained in such experiments will be of little value no matter how many of them may be reported in the future. Indeed, it may truthfully be said that such papers thus far have done more harm than good because of the acceptance of the erroneous conclusions by the average reader who has no time to examine the data critically. Perhaps even more serious is the fact that these extremely doubtful conclusions have been quoted without criticism again and again in later scientific papers, indicating that a thorough and critical examination of the experimental procedure and the results obtained in the earlier papers could not have been made. It cannot be overemphasized that valuable results in this field can be obtained only by long-continued experiments under accurately controlled conditions.

The aim of this discussion is to present a critical review of the work that has been done on the effects of ultraviolet radiation upon seed plants, with particular emphasis on the work of recent years up to the early part of 1932. The subject is subdivided as follows:

Part I. The effect of ultraviolet radiation upon seed germination and early growth of seedlings.

Part II. General and specific effects of ultraviolet radiation upon more mature plants.

Part III. Other effects of ultraviolet radiation upon seed plants.

¹ Contribution No. 80, Department of Botany, The Pennsylvania State College, State College, Penna. Publication authorized by the Director of the Pennsylvania Agricultural Experiment Station, Technical Paper No. 568.

PART I

THE EFFECT OF ULTRAVIOLET RADIATION UPON SEED GERMINATION
AND EARLY GROWTH OF SEEDLINGS

Before 1921 very few investigations had been carried out on the effects of ultraviolet radiation upon seed germination and early growth of seedlings. Carl (24) had stated that ultraviolet rays from a mercury vapor lamp were detrimental to seed germination and the early growth of plants. Raybaud (114, 115) on the other hand, had reported that the rate of germination of certain seeds was increased by such radiation, but that the seedlings were injured and died soon after emerging from the seed coats. Schanz (128) had found that seeds did not sprout as readily in daylight containing ultraviolet radiation as in daylight from which this radiation was screened out.

In 1921 Popp (106, 107) carried out investigations upon the effect of ultraviolet radiation upon seed germination and early growth of seedlings. In a series of experiments upon various types of seeds including foxglove, tobacco, mustard, corn, Canada field peas, lupine, and sunflower he made numerous tests using the mercury arc in quartz as the only source of radiation. In some cases it was used unscreened and in others screened by various filters. The length of exposure ranged from a total of one or two hours up to six to ten hours per day for several days. The ranges of radiation reaching the experimental plants were indicated by spectrograms. From 50 to 100 seeds were used in each test with a corresponding number of controls, involving a total of about 5,000 seeds. Plants were compared which had received approximately only the region 420 to 320 $m\mu$. plus some infra-red, only the visible and infra-red plus the ultraviolet down to 300 $m\mu$., and the visible and infra-red plus the ultraviolet down to about 200 $m\mu$. Intensity differences under the various experimental conditions were not recorded because instruments for measuring these were not available.

The experiments indicated that exposures of dry seeds to the entire radiation of a quartz mercury arc for as long as 188 hours had no effect on later germination and growth and that exposures of less than two hours of soaked seeds that had not yet begun to sprout had no effect on later germination and growth. This was explained as probably due to the failure of the short injurious rays to penetrate sufficiently to be effective. Longer exposures of soaked seeds were injurious, and wave lengths below 300 $m\mu$. were particularly harmful. No differences in rate of germination were noted in seeds grown in the dark, in the radiation of the lamp from which the ultraviolet was screened off, or under the lamp from which only

the ultraviolet below about 300 $m\mu$. was screened off. If, however, the principal radiation (aside from infra-red) the seeds received was ultraviolet of the approximate region 400 to 300 $m\mu$., injurious effects were indicated, more upon the seedlings after germination than upon the rate of germination, but these effects were probably chiefly caused by the absence of sufficient light for growth. Seedlings grown with the unscreened lamp as the only source of radiation never developed beyond the stage that would result from food stored in the seeds. This, plus the fact that starch tests on mature geranium leaves which had been irradiated, were negative, was thought to be an indication that food synthesis is slight under the radiation of the unscreened lamp.

From 1921 to 1927 the reports of Sibia (145), Russell and Russell (123), Dane (30), and Ritson (37) all indicated only injurious effects of the unscreened mercury vapor arc. Ritson's conclusion that germination of *Trifolium subterraneum* is delayed by short repeated exposures to the unscreened arc is hardly justifiable since the seeds were planted in the soil where ultraviolet radiation obviously could not have reached them. His observations on the seedlings after they had appeared above ground are, of course, not open to this criticism.

Beginning in 1927 Sheard with various co-authors published a number of papers on the effect of "general" and "selective" irradiation upon plants. Four of these (135, 67, 136, 137) deal with germination of seeds and early growth of seedlings. Since we find the conclusions of these authors repeatedly referred to as though they were established facts, it seems desirable to call attention to the manner in which they were reached. One is led to wonder whether those who have accepted the conclusions of these authors could have examined their papers critically.

In general the papers may be characterized as consisting of a minimum of experimental data on exceedingly few plants from which a maximum of conclusions and generalizations are drawn. In the four papers a total of 21 conclusions is reported. Of these the one most frequently quoted (67, conclusion 3) states that "wave-lengths ranging from about 320 $m\mu$. to 390 $m\mu$. seem particularly effective in inducing growth." The experimental data upon which this conclusion is based are recorded in the only table in this paper. A series of ten cultures, each containing six to ten cucumber seeds had been observed for about eight days. One of these cultures had been given short daily exposures to the full spectrum of a mercury arc in quartz, and hence received radiations as low as 200 $m\mu$.; one had been given daily exposures to the mercury arc screened by ordinary window glass which was said to transmit rays down to about 320 $m\mu$.; one had been given daily exposures to the mercury arc screened by vita glass which

transmits down to 270 $m\mu$.; and one had been given daily exposures to the mercury arc screened by ultra glass which was said to transmit only the region 320–390 $m\mu$. These, with a fifth control culture, were otherwise kept in the diffused light of a greenhouse as transmitted by the various screens with which they were covered. The control culture and the un-screened arc culture as well as the window glass culture had a window glass cover while in the greenhouse. The other five cultures paralleled the first five except that they were kept in darkness instead of in diffused light. Length of seedlings was the sole criterion by which the plants were judged. The longest seedlings were assumed to have been under the most favorable conditions. While the experiment was said to have been repeated five times, the data given are stated to be only “sample data which correctly portray the results which were found to occur under the experimental conditions cited in at least 80 per cent of the cases.” Anyone who has worked extensively with ordinary vegetable seeds, and particularly with cucumber seeds, knows that such seeds even under constant environmental conditions, exhibit wide variation in the rate of growth during the first few days of germination. Consequently data obtained from a quantity of six to ten seeds have little significance. The data given indicate, however, that the seeds under ultra glass did start to germinate a little earlier than any others. Yet the control culture in the dark not only overtook both ultra glass cultures but by the eighth day the length of these seedlings had exceeded by 12 mm. the length of the ultra glass seedlings kept in the dark, and by 42 mm. or over 100 per cent the length of the ultra glass seedlings in diffused light. The latter fact is overlooked by the authors. If the region 320–390 $m\mu$., the only region except infra red which is transmitted by the ultra glass, were beneficial, and if length of seedlings could be considered as a criterion of stimulation, as it was by the authors, it would seem that those seedlings receiving this radiation should have been longer than seedlings otherwise similarly treated except that they did not receive this radiation. Moreover, the ultra glass culture in diffused light supposedly received nothing but the region 320–390 $m\mu$., but more of it than the one in the dark, since it also received this region of ultraviolet in daylight as well as that present in the mercury arc spectrum. Yet the diffused light ultra glass seedlings were much shorter, only 57 per cent as long as those of the corresponding dark culture. The ultra glass diffused light culture could not, of course, be compared with the control in diffused light since the former received no visible rays and hence was etiolated as compared with the diffused light control which was not etiolated. It is difficult to understand how it could have been concluded from these data that the region 320–390 $m\mu$. was beneficial, even if the data were significant. Such

differences as are recorded are apparently different degrees of etiolation resulting from differences in total radiation, temperature, etc., etiolation being considered as "stimulation."

Conclusion 4 of this same paper (67) is the next most frequently quoted one. It states that "wave lengths of 270 $m\mu$. to 320 $m\mu$. appear to be inhibitory in their action." This is based upon the fact that the seedlings under vita glass were never as long as comparable seedlings under ultra glass. This "lessened growth" was ascribed in the discussion of the paper as due either to the "inhibiting effect of the visible light or the lethal effect of the lesser wave-lengths" transmitted by vita glass and not by ultra glass. In the conclusion, however, the possibility of the significance of the visible rays has been dismissed. In other words, lack of etiolation due to the presence of visible rays is interpreted as inhibiting action of the ultraviolet in the region 270–320 $m\mu$. It might be stated that while evidence from the accurate work of others does indicate that ultraviolet of wave lengths shorter than 300 $m\mu$. is inhibitory to plant growth, the data of these authors are in no sense a proof of it.

In paper 4 (137) we have the statement that "the infra red and red regions of sunlight, at one end of the spectrum, and the blue, violet and ultra-violet at the other extreme of the solar spectrum, are vital and stimulating to growth," and that "growth is greater under either the longer or the shorter wave-lengths of sunlight than it is under the full complement (practically) of sunlight." These statements are made without a single item of experimental data to support them; that is, *no data are given*. Even if we are to assume that the number of plants used and the methods employed were the same as in their papers that do give experimental conditions such conclusions are simply absurd.

Without going further into the remaining conclusions of these authors, suffice it to say that they are supported by no better evidence than the ones mentioned. Thus far Delf (36) is the only worker who has offered any specific criticism of the Sheard and Higgins reports. Delf has mentioned in a general way the disregard of light intensity differences.

In addition to the Sheard and Higgins reports about ten other papers since 1927 have reported favorable effects of ultraviolet radiation upon seed germination and early growth of seedlings. Ordinarily this might be interpreted as piling up of evidence in support of the original conclusion. That such is not the case, however, is clearly revealed by a careful examination of the papers themselves. Unfortunately misconceptions with small beginnings tend to grow as readily as correct ideas.

Brief reports in *Gardeners' Chronicle* for 1927 and 1928 by Maddock (81), Russell (122), and the Kew Gardens (70) state in general that better

results were obtained in houses covered with the English vita glass, which transmits all wave lengths of daylight ultraviolet, therefore down to 291 $m\mu$., than in houses covered with ordinary window glass, which transmits only down to about 313 $m\mu$. Vita glass is one of a number of glasses which have been put on the market since the region 291 to 313 $m\mu$. has been thought to be beneficial to higher animals. It is described in greater detail in the last subdivision of Part II of this review. The source of radiation in these experiments was daylight only. Russell states that seeds and seedlings when screened with vita glass germinated earlier and showed taller and sturdier growth than did those under ordinary glass, but no definite data are given in his report. In the Kew Gardens report it is stated, regarding germination that "the first lap of the race between two sets of seeds and plants . . . has ended in victory by twenty-four hours for those grown under the new glass which admits the ultra violet rays of the sun." Whether or not the seed stimulation refers to seeds which were planted is not stated. In addition, the mistake made in these papers is that of attributing the results to one variable, ultraviolet, when many other variables such as temperature, total radiation intensity, visible radiation, and infra-red radiation, also existed.

Valentin's experiments (166) were similar to those with vita glass reported above, except that he used Ultravit glass, a German product, instead of vita glass, to transmit all wave lengths of daylight ultraviolet. He compared school children, various chemicals, and the germination and growth of plants in two school-rooms having Ultravit glass windows, with those in two schoolrooms having ordinary glass windows. Corn, oats beans, and peas were put in each school room, eight seeds per room. These were planted in flower pots equally deep in the soil. ("Die Samen wurden gleichmässig tief in die Erde gebracht".) Because the seedlings in the pots behind Ultravit glass appeared above ground sooner than those behind window glass the conclusion of the author was that the earlier appearance of the one set of seedlings was due to stimulation of germination by the ultraviolet transmitted by Ultravit glass and not by window glass. It is difficult to understand how any ultraviolet could possibly have reached seeds buried in soil. Yet this obviously erroneous conclusion has been quoted by Masure (87) without comment. Further growth of the seedlings was somewhat better behind Ultravit glass than behind window glass. Additional comment on this is unnecessary.

Jacobi (68), after giving an extensive review of literature dealing with general effects of ultraviolet radiation, presents the results of his own experiments, some of which were concerned with seed germination. Radish, mustard, and lettuce seeds were selected for this work because they ordi-

narily give better germination in the dark than in the light. A mercury vapor lamp was used as the source of radiation. By the use of glass and solution screens, all other regions of the spectrum were eliminated, except the region between 300 and 400 $m\mu$. When dry seeds were exposed to this region for periods of 8, 16, 24, and 32 hours, no marked effect was produced on germination except that the mustard irradiated 24 hours and the lettuce irradiated 32 hours seemed to be furthered in growth after two days. Soaked seeds, on the other hand, irradiated for 2, 4, 6, and 8 hours were reported to give a somewhat higher rate of germination. Exposures of soaked seeds for 10 hours reduced the rate of germination. Seeds irradiated after the emergence of the radicle were unaffected by 2, 4, 6, 8, or 10 hour irradiations.

An examination of the data in which favorable effects of the radiation seem to have occurred shows wide variations and fluctuations in the rate of germination of irradiated plants as compared with controls. For example, after 66 hours the average percentage germination of lettuce irradiated for 2 hours was 65.5 while that of the control was 63.75 per cent, but this same seed irradiated for 4 hours gave 63.5 per cent germination in the same time, while the control gave 68.5 per cent. Furthermore, there is no consistent correlation between time of irradiation and effect. In one instance the 2-hour exposure gives the highest rate; in another the 6-hour one; in still another, the 8-hour one. While in many cases the controls were somewhat behind the irradiated plants in rate of germination, fluctuations are so great that it would hardly be justifiable to attribute this to a stimulating effect of the region between 300 and 400 $m\mu$.

Mezzadrolì and Varetton (93, 94) claim to have obtained favorable results on germination and the first stages of seedling growth by irradiating in an oblique direction, with ultraviolet of wave lengths 330 to 390 $m\mu$., obtained by screening a mercury arc with Wood's filter. The favorable effects were scarcely noticeable the first day, most conspicuous during the first days of seedling growth and diminished after about the tenth day. Although the authors report that numerous experiments were carried out on diverse plants for varying lengths of time, they give only four examples. One hundred barley seeds, 50 kidney beans, 25 peas, and 25 corn grains were irradiated 30 minutes per day at a distance of 50 cm. from the light source in an oblique direction. Of these only 41 barley seeds germinated, 30 kidney beans, 23 peas, and 13 corn grains. In the corresponding controls 31, 25, 19, and 10 seeds respectively germinated. It is difficult to understand why seeds giving such low percentages of germination should have been used in the first place. Measurements obviously were made on very small numbers of plants. Moreover there is no indication that en-

vironmental conditions aside from quality of ultraviolet radiation were equalized between experimental and control plants. In the experiment with the most seedlings there is practically no difference in average lengths of seedlings under the two conditions. The measurements are 48.8 mm. for irradiated and 48.4 mm. for non-irradiated seedlings. When fewer seeds were used the differences in average lengths of seedlings were greater, but it is doubtful that these differences were due to irradiation treatments. Average fresh weights of tops of seedlings at the end of 12 days for the control plants were uniformly as good as or better than those for treated plants. In the table published total lengths and total weights of seedlings are given, which might be misleading, since different numbers of measurements make up the totals in each case.

In a second paper are presented effects of the unscreened lamp. In general, damaging action of this treatment was noted, but at a distance of 50 cm. from the light source in an oblique direction with daily doses of one to five minutes duration, a slight excitation was noted, especially in plants kept in darkness. If the time of exposure was increased, instead of more marked favorable effects, the treatment caused injury. There is nothing very conclusive about these results, and the authors themselves are not very emphatic in their support of this method of obtaining favorable effects on seedlings.

Popoff (105) in his book on "Die Zellstimulation" reports general increase in rate of germination and better development of seedlings of rye and wheat under short exposures to an unscreened mercury vapor lamp. This "stimulation" in the case of soaked wheat seeds meant 96 per cent germination in the test plants as opposed to 92 per cent in controls. In other cases the differences were somewhat greater though of little practical significance. In any case, the conditions of the experiment indicate no provision for differences in environmental conditions aside from ultraviolet radiation, but the results are ascribed exclusively to ultraviolet radiation. Incidentally the author likewise finds that seeds are stimulated by chemicals, electricity, high frequency currents, radium, x-rays, hormones, and by various other means.

One of the most recent papers in which stimulation of early development of seeds is claimed is that of Masure (87). He has watched the behavior for four days of pea seeds kept in the dark after irradiation for various lengths of time with a mercury vapor arc in quartz through a Corning G586AW screen. The range of this filter was given as 3334 to 3690Å. with a maximum transmission in the region 3650Å.

In the introduction to this paper Fuller (49) is quoted as having tested some of the work of Popp and Brown and obtained considerable increase

in growth where they obtained negative results. Fuller's work, however, cannot be compared with that of Popp and Brown because the conditions under which his experiments were conducted were entirely different from those of the latter's experiments. Furthermore, Fuller worked with more mature plants whereas Popp and Brown, in the work cited, dealt exclusively with the effect of ultraviolet radiation upon seed germination and the early growth of seedlings. Fuller has in no way repeated the work of Popp and Brown.

In the summary of the paper only the possible demonstration of stimulation is mentioned, although earlier in the paper the author gives data which he himself states as indicating lack of stimulation. For instance, under no conditions of exposure in which the rate of germination was recorded did the irradiation of dry or soaked seeds influence in any significant degree the rate of germination. As stated by the author, "The results obtained allow only one conclusion to be drawn, namely, that raying has no marked effect on the rate of germination." Moreover, the data including average hypocotyl lengths of seedlings subjected to statistical analyses "do not indicate that the raying had a distinctly significant effect on the seeds."

The author's statistically significant figures indicating stimulation were obtained by comparing frequency distributions of root growth of seedlings of related pairs of lots of rayed and control populations. In this comparison the frequency distribution curves for a treated and a corresponding control lot were plotted on the same sheet of graph paper, and a comparison made of the shift of the treated relative to the control population. By thus abandoning "average growth values" as masking the effect of raying and resorting to statistically analyzed frequency distribution curves of root growth, he has obtained significant figures in favor of raying; that is, the percentage number of seedlings of rayed lots growing as fast as the fastest third of control lots was greater for rayed groups. While the statistical methods used seem to be satisfactory, the author has failed to give the data which would enable one to determine actual population distributions, upon which his only demonstration of stimulation is dependent. Furthermore, it cannot be overemphasized that while statistical analyses may show significant differences between test plants and controls, no statistical method in any sense indicates that one of a multiple of operating factors is the sole cause of the significant difference unless all of these factors are taken into account.

That variations between test plants and controls other than the presence or absence of ultraviolet radiation did occur in Masure's experiments is very probable. Certain measurements of the radiation used by Masure,

made in our laboratories with a Kimball and Hobbs pyrheliometer, indicate this. A sample of G586AW glass of the type used by Masure gave a total transmission of 10.71 per cent of the radiation from a Cooper Hewitt mercury vapor arc. When a sample of Noviol "O" glass was interposed between the mercury arc and the G586AW screen the transmission was 7.14 per cent of the energy incident on the Noviol "O" screen. Since the Noviol "O" glass transmits practically no ultraviolet, the 7.14 per cent transmission of these two glasses together must represent energy in the visible and infra red, though chiefly in the infra-red, since the G586AW glass transmits only very feebly in a small part of the extreme visible red. Since the transmission of G586AW alone was only 10.71 per cent of the total energy of the mercury lamp and since when all ultraviolet was removed the transmission was still 7.14 per cent, it is obvious that the ultraviolet transmission of G586AW could not exceed 3.5 per cent. If the absorption of infra-red by the Noviol "O" glass were taken into account, this figure would be reduced still further. When we consider that a large part of the energy from a mercury arc is in the ultraviolet and that when all this is eliminated, the G586AW filter still transmits 66 per cent as much energy as it does when the ultraviolet is present, we must conclude that the G586AW screen transmits infra-red better than it transmits ultraviolet. If then we get differences in germination under this screen it is hardly justifiable to attribute them to ultraviolet unless we have supplied our controls with an equal amount of infra-red. In any case, we can hardly agree with the author that his experiments were conducted in the absence of all other radiations than ultraviolet. While it is possible that very small differences in the ultraviolet might be more effective than large differences in the infra-red we cannot be certain of this until it has been demonstrated experimentally. If, as in the case of Masure's experiments, the differences are so slight as to require statistical manipulation to bring them out, we can reasonably doubt that the ultraviolet was very effective.

It might further be mentioned that some of the significant figures are based on averages of seedlings which received exposures ranging from 15 minutes to 72 hours. This is not a very satisfactory lumping of data. In other cases individual series were analyzed. One would expect that if the ultraviolet is the effective agent in producing beneficial results there would be some relation between time or intensity of exposure and the effect produced. Yet no relation is apparent.

Masure's experiments were conducted with seeds in closed dishes placed at distances of 8.5, 17.5, and 18 cm. from the mercury arc lamp. It is difficult to understand how a fan alone would prevent heating effects from the lamp at such short distances, especially under periods of irradi-

ation lasting several hours. In his lots H and K the seeds, in Petri dishes, were covered with G586AW glass and then brought to a distance of 8.5 cm. from the arc. Under these conditions heating effects must have been pronounced.

In view of all these considerations, we are far from convinced of the validity of the author's conclusion that "ultraviolet radiation of 3650 Ångstrom units wave length, in the time and intensity employed and in the absence of all other radiations throughout the experiment, exerts a stimulative action on the subsequent rate of growth of the hypocotyl of pea seeds irradiated in the air-dry state."

Since 1927 there have also been those who have reported harmful or indifferent effects of ultraviolet on seeds and seedlings. Unscreened arc experiments in general have yielded such results and have failed to show beneficial effects.

Popp and Brown (109, 110, 111) have over a period of years carried out experiments on seed germination and early growth of seedlings using chiefly turnip and also radish, cucumber, pigweed and curled dock. These were reported in part at the New York meeting of the Botanical Society (110). Over 12,000 seeds have been used in these experiments. No less than 50 seeds per culture were ever used in any test. Fifteen different series of experiments have been completed. The seeds were usually germinated on moist filter paper and cotton and kept, except for short daily exposures to the mercury vapor arc, some in the dark, some in diffused light, and some in diffused light minus all ultraviolet. Irradiations were given with the unscreened arc and with the arc screened with various Corning filters including Noviol "O" which excludes practically all ultraviolet, G586A, which absorbs practically all visible and transmits the ultraviolet region between 320 and 400 $m\mu$., Corex, which excludes ultraviolet below 270 $m\mu$., and window glass which excludes ultraviolet below 313 $m\mu$. In addition, some cultures were exposed to the ozone only of the lamp. The irradiations were usually given for ten days when rapidly germinating seeds were used. A special effort was made to provide adequate controls.

The outstanding results of these experiments have been (1) the marked and invariably injurious effect on seedlings of the radiation of the unscreened arc even for exposures as brief as one-half minute per day, (2) the lessened injurious effect of the radiation through a Corex filter, and (3) the failure of any region of the ultraviolet studied to influence significantly the rate or the percentage of germination or to stimulate the growth of seedlings. It should be emphasized that *no significant stimulation was ever obtained when adequate controls were used*. The effects were recorded by general appearance of cultures, hypocotyl lengths, leaf measurements, and dry weights.

Cluzet and Kofman (26) irradiated dry barley grains with a mercury vapor arc in quartz at a distance of 60 cm. for from 3 to 4 hours with no effect on the later development of the seedlings. Germinating seeds, however, irradiated from 3 to 5 minutes every two days showed after the first day of such treatment a discoloration of leaves followed soon by retardation of stem growth. In no case was any acceleration of growth noted. To determine whether there exists an antagonistic action between x-rays and ultraviolet rays seedlings were submitted to ultraviolet rays, the germinating seeds of which had formerly received feeble doses of x-rays. Not only did the ultraviolet not prevent the harmful action of x-rays but it accentuated it, adding its harmful effects to those of the still shorter x-rays.

Mezzadrolì and Vareton (94) have reported harmful results of the unscreened arc with exposures of one minute or more at distances of 50 cm. or less, the injury increasing with decreasing wave length and increased length of exposure to the point of death. The data reported on hypocotyl lengths, however, are not very convincing one way or another except that a much smaller number of seedlings was averaged in the unscreened arc cultures. These authors also report (93) injurious effects of the region 330 to 390 $m\mu$. if exposures are made at short distances, but no data from such irradiation are presented.

Pires de Lima (104) reports unfavorable results from the irradiation of dry rye seeds, seeds soaked in water, and seeds soaked in eosin solution exposed to a mercury arc at 30 to 80 cm. for single periods of 5 to 30 minutes and observed for one month afterward.

Tincker (156) found no differences in the rate of germination of certain vegetable seeds in frames with ordinary glass, vitra glass and another ultraviolet transmitting glass. Whether the seeds were covered with soil was not stated.

Detwiler (38) reported that the exposure of dry seeds of *Ribes rotundifolium* to ultraviolet of 270 to 320 $m\mu$. delayed germination and caused pronounced stunting of seedlings. The duration of the injury, after irradiations were discontinued, was proportional to the length of the treatment.

Viewing collectively the experiments thus far carried out on the effect of ultraviolet radiation on seed germination and the early growth of seedlings, we observe that the only fact clearly demonstrated is the injurious effect of short-wave radiation, that below 290 $m\mu$. While there is some indication that certain ranges of ultraviolet might be beneficial in one way or another, the results so far reported are far from conclusive, and the evidence from more carefully controlled experiments would indicate little or no effect of the longer wave-lengths, those from 290 to 400 $m\mu$.

PART II

GENERAL AND SPECIFIC EFFECTS OF ULTRAVIOLET RADIATION UPON
MORE MATURE PLANTS

In the preceding paragraphs we have considered investigations dealing only with the effects of ultraviolet radiation upon seed germination and the first stages of seedling growth. Investigations dealing with effects on plants in more advanced stages of growth and on plants under observation for considerable periods of time will now be reviewed.

Experiments of this nature have been carried out in various ways. In some, the effects of single exposures or several exposures to a mercury vapor arc have been noted. In others, plants have been grown for considerable periods in daylight from which all ultraviolet rays have been eliminated by appropriate screens. In others, plants have been grown for a number of weeks under ordinary greenhouse conditions with additional short daily irradiations from a mercury arc in quartz either unscreened or covered with one of several filters. In others, artificial illumination only has been used, in combination with various filters. In still others plants grown in houses, frames or boxes with ordinary glass panes have been compared with plants under similar conditions except that the ordinary glass panes were replaced by one of a number of special ultraviolet transmitting glasses.

The results of the various experimental procedures have been recorded in a number of ways. The criteria most often used were general appearance of the plant, evidence of necrosis, height of plant, number and size of leaves, time and amount of flowering and fruiting, fresh weight, dry weight, and ash content. In addition, stem diameter, pigment development, development of spines, hairs, etc., anatomical features, chemical composition, enzyme development, and various other criteria have been used.

The discussion of the reports falling into this group is subdivided into investigations dealing with:

1. Injurious effects of short-wave ultraviolet radiation.
2. Plants grown in daylight from which the ultraviolet portion was removed.
3. Plants grown in daylight with additional short daily irradiation from a mercury vapor lamp.
4. Plants grown exclusively under artificial illumination.
5. Plants grown under special ultraviolet transmitting glasses.

*Investigations dealing principally with injurious effects of short-wave
ultraviolet radiation*

Earlier works such as those of Siemens (146), Déhérain (35), Bailey (9, 10, 11), Bonnier (17), and Rowlee (121) with electric arc light will be

passed over. The works of Hertel (64, 65), Maquenne and Demoussy (82), Kluyver (71, 72), Stoklasa (150, 151, 153), and Ursprung and Blum (165) appeared a little later. These investigators all noted the superficial destructive action of the short-wave ultraviolet. Kluyver (73) emphasized for the first time that the destructive rays were not present to any appreciable extent in solar radiation.

More recently Arthur and Newell (8) have performed experiments to determine what region of the ultraviolet is most injurious and whether that region near wave length $290\text{ m}\mu$., the extreme limit for solar radiation, is injurious to plant tissue. Using a quartz mercury arc and a series of Corning filters which absorbed progressive increments of the extreme ultraviolet radiation between wave lengths 200 and $290\text{ m}\mu$., they noted the time necessary to produce marked injury on young tomato plants. Spectrograms and transmission curves, after continued use of the filters, were given so that the nature and amount of ultraviolet actually reaching the plants were definitely known. In addition, the total radiant energy reaching the plants through the various screens was measured by a Weather Bureau type pyrheliometer. Not more than 6 per cent variation was found to occur. Provisions were made for maintaining the constancy of the radiation of the mercury arc. The filters used were found not to solarize. Hence these experiments were performed under carefully controlled and relatively definitely known conditions of radiation.

The results showed that the time of exposure to the arc necessary to cause marked injury increased rapidly as more and more of the extreme ultraviolet component was cut off from the plants. By means of a quartz concentrating lens which increased the intensity three-fold it was also shown that apparently the time of exposure necessary to cause marked injury with a given quality of radiation is approximately inversely proportional to the incident energy. The injury produced was found not to be cumulative. That is, a plant but slightly injured by a single irradiation of a given duration through a certain filter received little further injury when irradiated through that same filter each day for several weeks for that same length of time. However, since new tissue is continually forming as the plant grows, the total injurious effect produced on a plant was much greater when it was exposed often than otherwise. No marked beneficial effects were observed in any of these experiments. Nor was any injury produced within the extreme limits of wave-lengths present in solar radiation except under conditions which never occur in nature, namely, irradiation through a concentrating lens and a screen transmitting faintly to $289\text{ m}\mu$. for $16\frac{1}{2}$ hours. Injury did result, however, from wave-lengths but slightly shorter than those occurring in solar radiation.

These results indicate that the so-called incremental method of exposure used by Eltinge (43) and Fuller (49) is of no significance as regards its allowing the plant to become accustomed to radiation. Fuller has theorized rather elaborately on the possible benefits of such a plan, although it apparently proved successful only in a preliminary experiment of his and not in his principal experiment. Results of experiments by the authors of this review (111) also indicate that the incremental method is no different in its effect from one in which equal daily exposures are given as far as accustoming the plant to radiation is concerned. Each irradiation is effective independently of all others.

These results also indicate the incorrectness of Fuller's conclusions in his last brief experiment on infra-red radiation (50) in which he states that the infra-red is responsible in considerable degree for mercury arc injury. This will be pointed out in more detail later.

Finally, these carefully conducted experiments confirm once again and more accurately than previous experiments had, the results of earlier workers who have obtained injurious effects with short-wave ultraviolet radiation.

Investigations dealing with plants grown in daylight from which the ultraviolet portion was removed

Schanz (128) concluded that the elimination of the ultraviolet was beneficial to plants and recommended Euphos glass, which excludes ultraviolet, for greenhouses. His failure to take into consideration light intensity differences makes it doubtful whether his results were really quality effects.

Popp (108) in 1925 conducted experiments at the Boyce Thompson Institute. Here for the first time seed plants were grown in light of various ranges of wave-lengths under controlled and stated conditions, particularly with regard to light intensity and quality. When only the ultraviolet portion of solar radiation was removed by a Noviol "O" screen of the Corning Glass Works, no significant effects were produced on plants as evidenced by general appearance, development of pigments, rate of growth, time and amount of flowering and fruiting, fresh and dry weights, amount of total carbohydrates, starch content, total and soluble nitrogen, and some of the higher organic compounds. Any indications given were in favor of the elimination of the ultraviolet. If, however, the blue end of the visible spectrum was removed with the ultraviolet, then decidedly abnormal plants resulted.

The experiments of Shirley (143) have indicated that the blue violet end of the solar spectrum is more efficient in dry weight production than

the red end, when light intensities are uniformly 10 per cent of that outside. The removal of the ultraviolet and some violet, however, caused no very significant decrease in efficiency, which is to be expected when we consider the small percentage of total radiation in this region.

Jacobi (68) attempted to determine whether the formative effects of ultraviolet radiation such as dwarfing, hairiness, thicker and smaller leaves, brighter colored flowers, etc. claimed by Schanz (127) were really ultraviolet effects or whether they were light intensity effects. He grew plants under Uviol, an ultraviolet transmitting glass, and Euphos, an ultraviolet absorbing glass, under solar radiation, and then sought to confirm his results as quality effects by performing laboratory experiments with artificial illumination in which an attempt was made to equalize intensities. He concluded with Schanz that the dwarfing effects were quality effects caused by ultraviolet radiation. He went still further and determined fresh and dry weights of his laboratory plants. Fresh weights came out in favor of Euphos glass, and dry weights in favor of Uviol glass, which was thought to be an indication that ultraviolet favors dry weight production. However, the fact that fresh weights came out in favor of the Euphos glass, is an indication that one might justly be suspicious that intensity differences in radiation were in operation. There are no figures given of the actual intensities reaching the experimental plants in that part where the attempt was made to equalize intensities. It might be noted that Senn (133) has attributed dwarfing in alpine regions to greater light intensity there, but he gave quality no consideration.

The experiments seem to indicate that at low altitudes the elimination of solar ultraviolet alone has relatively slight if any influence on the plant. At higher altitudes where solar ultraviolet is more intense or under artificial radiation rich in that portion of ultraviolet present in sunlight there are indications of possible formative effects of ultraviolet, although these have not been clearly separated from intensity effects in the visible, particularly in the blue violet region. Shaw (134) and later Popp (108) have emphasized the significance of the blue end in relation to configuration of the plant.

Simon (147) in a recent semi-popular account of the nutrition of cultivated plants mentions incidentally an experiment of his with Euphos glass of the type used by Schanz. Cultures of garden plants under this glass were said to give, under otherwise similar conditions of environment and nutritional conditions, increased yields up to 50 per cent over plants grown under ordinary glass. The author, however, gives the impression that he was of the opinion that Euphos glass transmits ultraviolet better than ordinary glass does. If it was, as stated by the author, the same glass as

was used by Schanz, it *eliminated* the ultraviolet. An accurate statement of the conditions of the experiment is not given. In view of the many claims made recently for ultraviolet we wonder whether the author's results would have been as striking had he known the real transmission of this Euphos glass.

Investigations dealing with plants grown in daylight with additional short daily irradiation from a mercury vapor lamp

A glance at Tsuji's short preliminary paper in the Louisiana Planter (162) would convince any critical observer of the inconclusiveness of his extravagant claims. We mention the paper here merely because it has been referred to in later reports.

Delf, Ritson, and Westbrook (37) in 1927 attempted one of the first studies of the effects of short daily exposures of plants to the radiation of an unscreened mercury arc. Young plants of *Arachis*, *Voandezia*, and *Trifolium* exposed at various distances for short periods up to ten minutes per day were stunted, the epidermis of the leaves collapsed, and leaf mesophyll was less differentiated and more compact than in the controls. All of the irradiated plants died after the conclusion of the experiment. Of ten controls left, five were irradiated for one month for 30 seconds per day at a distance of eight feet. Two months later the irradiated plants were larger and more vigorous than the controls. As there were just five of these plants, the results were considered only "suggestive." They were never repeated. Harmful effects were obtained in various other experiments and were more marked on plants given shorter daylight illumination per day than on those given longer periods in the light.

Eltinge (43) has set down observations on rooted cuttings and young seedlings of plants grown for a number of weeks under ordinary greenhouse conditions with additional daily irradiations from a mercury vapor lamp at distances of 50 and 100 inches. Plants were exposed to the unscreened lamp, to the lamp covered by vita glass which was said to transmit down to 289 $m\mu$., or to the lamp screened by quartzlite glass which was said to transmit down to 313 $m\mu$. The irradiations were given by the incremental method, that is, for a period of one half minute the first day and for periods increasing by one half minute each day, on succeeding days.

While a considerable total number of plants was used, there were too many different species under too many different conditions so that generally no more than six to ten individuals of a given species were given a similar treatment. Average figures recorded in tables, therefore, are computed from data on six to ten plants grown under variable environmental conditions for from four to eight weeks. While all of her beneficial results

were attributed to ultraviolet radiation, she had no controls to eliminate the possibility of visible, infra-red, temperature and other effects of the lamp, since her so-called controls received no irradiation whatsoever from the lamp. Furthermore she made no measurement of the quality or intensity of ultraviolet reaching her plants under the various conditions used.

The only consistent result of treatments was injury by the unscreened arc to all plants used. Individual groups of plants irradiated through vita glass or quartzlite glass did prove superior to non-irradiated plants in a number of cases, but the differences were often slight and no one type of glass gave uniformly better results. The superiority expressed itself differently in almost every set of plants in which it appeared. It might be greater height, greater thickness of stem, larger leaves, greater number of leaves, greater average rate of growth, greater rate of growth during the last days or during the last weeks of the experiment, earlier flowering, or better color of plant. There were various combinations of these features. The same treatment caused stimulation in one respect and retardation in another. For instance, no type of irradiation proved superior to controls for *Raphanus* and *Nicotiana*. For *Bryophyllum* and *Phaseolus*, vita glass and a distance of 50 inches from the lamp proved best. For *Coleus*, vita glass and 100 inches was best. For *Zea Mays*, vita glass and a distance of 100 inches, and quartzlite glass and 50 inches distance from the lamp gave equally superior results. For *Lactuca*, quartzlite glass and 50 inches distance from the lamp caused the most leaves to develop, but they were smaller than those of controls. Cultures under vita glass at 50 or 100 inches had fewer leaves than those under quartzlite at 50 inches, but more and slightly larger leaves than control cultures. For *Cucumis*, vita glass and 50 inches distance proved superior for stem elongation, but the control plants had more leaves. For *Ipomoea* quartzlite and 100 inches distance proved best for stem growth, but quartzlite and 50 inches were equally as good as quartzlite and 100 inches for leaf number, and both were better than controls. To illustrate the effect of the same irradiation treatment on three different sets of plants, the results of irradiation through vita glass at a distance of 50 inches may be cited. For *Zea Mays* at first the control plants grew taller, but during the last few days the rayed plants grew very rapidly and surpassed the controls. Rayed stalks were larger in diameter, rayed leaves outnumbered control leaves and were larger. For *Nicotiana*, however, the observations pointed toward a retardation of growth, though there was no evidence of burning. For *Ipomoea*, little difference was noted between rayed and control plants although the rayed plants had more leaves.

Such results point far more likely to differences resulting from inherent

variations of the plants themselves coupled with environmental variations of one type or another not taken into account. Certainly we should hesitate to attribute such varied effects solely to one variable under the conditions used in her experiments. Miss Eltinge's conclusion that "each plant has its own ultraviolet requirement for best growth which can be determined only by experiment" rests upon the assumption that the ultraviolet was the only variable in the test plants as compared with the controls. This obviously was not the case.

From the Michigan Agricultural Experiment Station (2) comes the report that four minute daily exposures of soybeans and tomatoes to ultraviolet radiation down to 200 m μ . at a distance of one meter from a mercury vapor lamp caused injury in every case. The conclusion that a daily treatment of one minute at 9 A.M. increased the dry weight 10 per cent while a similar treatment at 3 P.M. resulted in a 7 per cent decrease is difficult to comprehend. Unfortunately this is just a progress report and no data are given which would enable one to interpret the effects reported.

Hey and Carter (66) tested the effect of the Hanovia Artificial Alpine Sun Lamp at 48 inches for periods of one and three minutes daily on the vegetative growth of wheat seedlings and their infection by *Erisiphe graminis*. They report no stimulation of growth for the variety "Little Joss," but uniformly taller and stronger plants in one experiment with the "Persian Black" variety. This, however, was not verified in a second experiment in which no stimulation was evident. A three minute daily exposure greatly reduced infection by mildew on the susceptible variety "Little Joss." When the treatments ceased, the plants again became infected. The authors attribute suppression of fungus growth in wheat fields in hot dry summers to the increased amount of ultraviolet present in solar radiation and its increased growth in wet weather to the decreased amount of ultraviolet present. One of the serious errors in this generalization is that solar ultraviolet is different in quality and intensity from that of the artificial source used.

To date Fuller has published four times. The first report (48) was a brief summary in "Science" of work which was later reported more fully in the "Annals of the Missouri Botanical Garden" (49). The third, with Wynd as co-author (173) was a brief report on analyses of the ash of some of the plants used in one of the earlier experiments. The fourth (50) was a note on the effects of infra-red as compared with ultraviolet effects of a mercury vapor lamp. His work has been with young tomato and cucumber plants.

The first three reports are based upon one preliminary and one major experiment in which untreated plants in a greenhouse were compared for

several weeks with plants given daily irradiations from a mercury vapor lamp either unscreened, screened with vita glass, or screened with quartzlite glass. The daily periods of irradiation were either constant for 7.5 or 9 minutes per day or incremental, starting with one half minute per day and increasing by one half minute each succeeding day. The similarity to Eltinge's procedure is evident.

In the first experiment only 15 plants per treatment were used. In the second and principal experiment 100 plants per treatment were used. The injurious effects of the unscreened arc were again noted. In addition, stimulation of plants by ultraviolet radiation is claimed as evidenced by increased height, number of leaves, fresh weight, dry weight, ash weight, and calcium content, over controls. Tests on phosphorus content were also made, but no increase was noted in irradiated plants. Although the author states in his summary that "statistical analyses proved the reliability of the results" of his major experiment he has not statistically analyzed plants which varied in treatment only in the quality of ultraviolet radiation received, and therefore his statistical analyses are not significant as indicating ultraviolet effects.

The "controls," as far as can be gathered from the data, were kept constantly in the greenhouse. The test plants were irradiated daily with a mercury vapor lamp. In these irradiations the plants received not only additional ultraviolet radiation not received by the controls but also additional visible and infra-red radiation as well as ozone. Moreover, the plants irradiated under vita glass and under quartzlite glass were under conditions which differed not only in the quality of ultraviolet present as was assumed, but also in the total intensity of ultraviolet present, and in the quality and intensity of visible and infra-red. Furthermore no attempt was made to record differences in intensity of radiation received by the plants compared except for total radiation intensities under the various conditions. Yet the author assumed that the one variable in his experiment was quality of ultraviolet, made his statistical analyses and drew his conclusions on this false assumption. This is strange in view of the fact that he has stated in the introduction of his principal paper (49) that "it is a flagrant disregarding of facts to assume that the effects of the mercury arc on organisms are due to the ultraviolet region alone."

Examination of data as recorded gives additional reason for questioning the validity of the conclusions. It is difficult to understand why the author concludes regarding the method of irradiation that "the incremental method for the most part produces greater growth than the constant period method, indicating an induced adjustment of the plants to the gradual increase of dosage" when, in the principal experiment only six tests out

of sixteen on height, number of leaves, fresh weight, and dry weight indicated better results for the incremental method as compared with the constant period method, and when his most outstanding favorable effects were obtained with plants irradiated by the constant period method. Previous work (8) has demonstrated that if, for example, one dose of ten minutes is injurious, previous exposures of the plant to smaller doses will not prevent injury by a ten minute dose later. We have tested out this method in our own laboratory and have obtained no better results by the use of the incremental method.

The only very outstanding experimental result reported in the first three papers is the better growth of plants under vita glass given constant daily exposures of nine minutes per day as indicated by height, number of leaves, and fresh weight. For tomatoes the dry weight percentages of fresh weights also were greatest under these conditions. For cucumbers, however, the dry weight percentages of the vita glass constantly exposed plants were less than those for both vita glass and quartzlite glass incrementally exposed plants by 0.1 per cent and 0.03 per cent respectively. These are not very great differences. The other results show fluctuations in no very consistent manner, the plants being in no great degree different from each other. It appears doubtful whether the irradiation treatments alone influenced the variations. In the principal one of these three experiments four sets of 100 plants each of cucumbers and tomatoes were irradiated at 100 inches from the mercury vapor lamp, two through quartzlite screens and two through vita glass screens. One set under each screen was irradiated for nine minutes daily and the other for one half minute the first day and a period increasing by one half minute each succeeding day. Through quartzlite glass the constant method of exposure gave the best stem growth in tomatoes, but the control plants and the incrementally exposed plants proved superior to the constant period plants for cucumbers. The control cucumber and tomato plants had more leaves than those exposed by the constant method, but fewer than those exposed by the incremental method. Fresh and dry weight percentages of irradiated plants in all experiments were greater than those of the control plant weights; but cucumbers gave the greatest fresh and dry weights by the incremental method while with tomatoes the constant period method proved superior. No ash analyses were made of these plants. If the vita glass incremental cultures are brought into the comparison the cucumber cultures proved inferior to all other cultures including controls in height, inferior to all other cultures except quartzlite constant period cultures in number of leaves, superior to all others except vita glass constant period cultures in fresh weight and superior to all others in dry weight. Tomatoes incrementally exposed under

vita glass, on the other hand were better than controls, about equal to quartzlite incrementally exposed plants, and inferior to other plants in height, superior to all except vita glass constant period plants in number of leaves and in dry weight, but exceeded by quartzlite and vita glass constantly exposed plants in fresh weight. Such variation within small limits offers no very convincing proof of beneficial effects of ultraviolet radiation. Whether the irradiation was the cause of the greater size of the plants in the vita glass cultures under the constant period method was never checked by a repetition of the experiment. Certainly that the ultraviolet portion of the irradiation was the determining factor was in no way proved because of lack of adequate control plants and lack of accurate measurements of the radiation reaching the plants. Since the ash analyses for calcium and phosphorus content were made with some of the control and vita glass constantly exposed plants of the experiments just referred to, the same criticisms hold true for the results given in this paper as in the one above, namely, that comparisons were not made between plants which differed in treatment only in the quality of ultraviolet received.

In the fourth paper Fuller concludes from an experiment with twelve tomato plants per culture, with three cultures that the injurious effects of the open arc at short distances are due in considerable degree to infra-red radiation from the arc. Here again the author has worked with relatively uncontrolled conditions with regard to the radiations under consideration. He assumes that interposing a 1.5 cm. quartz water cell between the mercury arc and the plants caused no diminution in the intensity of the ultraviolet reaching the plants as compared with the unscreened lamp. That this is not true is indicated by an examination of the coefficients of absorption of water in the ultraviolet as given in the International Critical Tables. In addition, measurements made in our laboratories with a Westinghouse P.E. Ultraviolet Meter indicate that the ultraviolet intensity is cut down 25 per cent in passing through such a cell. Furthermore, the shorter the wave-lengths the greater is the absorption. Thus the destructive radiation is reduced much more than the longer, less destructive radiation. Obviously the diminished injury by irradiation through the water cell cannot be assumed to be due merely to the elimination of infra-red.

Furthermore, a number of investigators have demonstrated that the more the short waves of the open arc are cut off from plants by appropriate screens, the less injury is there to the plants. Arthur and Newell (8) under very carefully controlled and measured conditions of radiation have shown this. They, as mentioned previously, used filters which absorbed progressive increments of the extreme ultraviolet component from the lamp to-

ward wave-length 290 $m\mu$. The time of exposure necessary to cause injury increased rapidly as more and more of the extreme ultraviolet was absorbed by the filters, yet the difference in total transmission through the various filters, including the infra-red transmission, was very slight, varying no more than 6 per cent. The possible injurious effect of infra-red radiation of high intensity is by no means denied, but Fuller's experiments do in no way indicate that the injurious effects indicated for short-wave ultraviolet by the more accurately controlled experiments of previous investigators are without foundation. If Fuller actually wished to demonstrate injurious effects of infra-red it is difficult to understand why he did not expose some plants to the infra-red in the absence of all ultraviolet.

Popp and Brown (111) in addition to previously reported experiments have carried out five series with buckwheat. In two of these, 2-minute daily exposures to radiations from a mercury arc were given for ten days; in the other two, half hour daily irradiations were given. In one 2-minute series and one half-hour series the seeds were planted in soil and the first irradiation given when the seedlings were several inches high. In the other two series the seeds were placed on moist filter paper and cotton and irradiated for the first time three days later, that is, after the seeds were well germinated. Fifty seeds per culture were used. Exposures were given to the open arc, to the arc screened by Corex glass, by window glass, by Noviol "O" glass and by G586A glass. In addition one culture was kept in diffused light with no irradiation, and one was exposed to the ozone only of the lamp. No favorable effects of the ultraviolet used in these experiments were obtained. The injurious effect of the unscreened arc was again manifested.

Investigations dealing with plants grown exclusively under artificial illumination

Withrow and Benedict's experiment (170) was unique in that they grew tomato and *Coleus* plants from seed for a period of three months under artificial illumination as transmitted by various cellophane filters. Theirs was an attempt to determine whether the region 290 to 313 $m\mu$., that region said to be of such importance to animal life, was essential for optimum conditions of plant growth. They state that others have failed to obtain stimulation either because they did not have present a sufficient intensity of the rays 290 to 313 $m\mu$., if daylight was the source of radiation, or that in addition to a sufficient intensity of the rays 290 to 313 $m\mu$. there were also present some of the shorter lethal rays, if the mercury arc was the source of radiation. In the use of artificial radiation they have a controlled light source with considerable intensity in the ultraviolet region.

They used cellophane filters especially developed for the experiment (169) the transmission curves of which showed sharp cut-offs at the desired wave-lengths, a quality said not to be possessed by many glass filters which have been used. Their results indicated to them that "the removal of the 2900–3100 Å. ultra-violet region is detrimental to the growth of tomato and *Coleus* plants, and that the inclusion of a small amount of lethal radiation of shorter wave length than 2900 Å. is sufficient to mask the beneficial effect of the 2900–3100 Å. region." This was indicated by the greater height and growth rate, greater internodal length, greater stem diameter, greater number and average area of leaves, and greater fresh and dry weights of those plants which received radiation in the region 290 to 310 mμ., with no shorter ultraviolet present. The final statement in the paper, however, reads that "because of the limited number of plants used and the inadequate growth conditions, especially with regard to intensity of illumination, these results are offered simply as preliminary data, indicating the possible growth-promoting action of the 2900–3100 Å. ultra-violet region."

Unfortunately the total light intensity was only about 30 foot-candles, an intensity so weak that it resulted in etiolation of the plants. None of the plants, therefore, was normal, except the so-called controls which were kept in the diffused light of a window sill with a southern exposure. These "controls" were not used in any of the measurements, and justly so since they were under conditions totally different from those of all other plants. While the cellophane filters used in this experiment were said to be stable, they were also said to show slow deterioration under intense irradiation. No further indication is given of the degree of stability of the filters. No measurements of total energy under the various screens are given. Such measurements would have been of particular value since the illumination intensity was probably below the minimum for normal growth and hence small differences in the different compartments might have caused pronounced effects on the plants.

The data recorded represent for tomato comparisons of measurements on 2, 6, and 14 plants respectively, and the fourteen plants under supposedly identical conditions show average measurements per pot to be more variable than average measurements of plants under different conditions. The tomato data are obviously of little value. The *Coleus* data were obtained by picking out three "representative" plants from each of five pots of *indefinite numbers of unthinned plants* under each condition. The photographs of these plants show decided crowding in the pots which is very unfortunate particularly when the illumination intensity was extremely low. It is difficult to understand why so many plants were used

per pot and on what basis any of the plants in any pot could be considered "representative." The photographs show that in any pot there was extremely wide variation in size of plants. Such data also are of limited value. There was no repetition of any of this work. While there is a possibility in these experiments of the favorable effect of the region 290 to 310 $m\mu$., the conditions under which the experiments were conducted were such as to offer very legitimate reason for doubt of the conclusions arrived at.

Investigations dealing with plants grown under special ultraviolet transmitting glasses

Since the region 290 to 313 $m\mu$., that region of the solar ultraviolet which is not transmitted by ordinary window glass, has been emphasized as necessary for the normal development and health of higher animals, a series of special ultraviolet transmitting glasses has been developed and put on the market. Various Corning glasses of this country and vita glass of England are among these. There are also numerous German glasses known by various trade names such as Uviol glass of Schott and Genassen, Jena; U-glass of Dresden, Ultraviolet glass of Berlin, Ufau, Ultra, Brephos, Ultravit, Sendlinger, Bios, and Sanalux glasses. Probably the Jena glass-works of Germany antedates all others in manufacturing ultraviolet transmitting glasses, having made them as early as 1903. Their Uviol glass in comparison with five other German glasses was found to transmit further down in the spectrum than any of the others and to transmit a higher percentage throughout in the ultraviolet than any of the others.

These new glasses differ from each other considerably in ultraviolet transmission and in addition some of them solarize, that is, lose a part of their transmission in the ultraviolet upon exposure to light (8, 44, 171, 172). This solarization is far more marked when the glass is used under a mercury arc than when used in ordinary sunlight. In a few cases glass substitutes have been tried, but these usually have not been found as satisfactory as glass screens (8) (169, 29). It is obvious that when one of these screens is used, the actual quality and intensity of the ultraviolet reaching the plants is questionable unless definite measurements are made regarding its transmission from time to time.

Unfortunately, not only is the ultraviolet transmission of these glasses different from that of ordinary glass, but so also is the visible, and in great degree the infra-red transmission. These features have been indicated by transmission curves of the glasses and by the temperature differences occurring under the two types of glasses. Any effects, therefore, obtained under one of these new glasses, cannot justifiably be said to be ultraviolet effects, but must be attributed to the difference in total transmission of

the glasses used, other environmental conditions being constant. Yet the majority of investigators who have used these new glasses have placed the emphasis on their relatively greater ultraviolet transmission.

Many of the experiments conducted with these new glasses have not been carefully controlled aside from radiation conditions so that results are correspondingly inconclusive. The fact that a small number of plants was used in many cases is also unfortunate, and failure to repeat experiments, still further reduces the value of results obtained since very often those who have repeated their experiments were unable to duplicate their original results. Most of the experiments of this type have been carried out from a practical viewpoint by greenhouse keepers, horticulturists, and floriculturists with practical results rather than scientific data as the aim and purpose.

In this country one of the carefully performed experiments of this nature was carried out at the Boyce Thompson Institute (6). Several species of flowering plants were grown under Uviol glass which transmits 80 per cent at the extreme ultraviolet of sunlight and no differences were observed in growth habit, time and amount of flowering or amount of green tissue produced as compared with plants grown under ordinary greenhouse glass. "We have yet to find any distinct advantage to the plant in growing it under a glass which transmits the extreme ultraviolet region of sunlight."

Osmun (99, 100) obtained favorable results under vita glass for lettuce and radish one year, but during the next year continued experiments gave contradictory results. The first year, radishes under vita glass showed a gain of 71 per cent in weight of the entire plant and 124 per cent in weight of roots as compared with an equal number of plants under ordinary glass. Similarly lettuce gained 76 per cent in weight and formed more compact heads under vita glass. The next year radishes averaged 10 per cent less in weight under vita glass than those under ordinary glass in one test and 14 per cent more in another. Lettuce under ordinary glass this second year weighed 3 per cent more than that under vita glass. Obviously nothing concerning ultraviolet radiation can be concluded from these results.

Tottingham and Moore (159, 160, 161) have reported on horticultural investigations at the Wisconsin Agricultural Experiment Station. In the principal paper (161) a small number of plants of twelve different species which had been under vita glass for a number of weeks was compared with plants similarly treated but grown under window glass. The comparisons involved the nature and amount of growth, dry weights, and partial chemical analyses. As stated by the authors "The present investigation is concerned with the elimination of a small portion of ultraviolet (about 3100

to 2900 Å.) in sunlight by the screening effect of common glass," but there is no mention in the summary of any favorable results under vita glass being due to the region 290 to 310 $m\mu$. alone. Favorable results mentioned for plants grown under vita glass are ascribed rather to "the more extensive irradiation under vita glass," and there is mentioned the desirability of separating infra-red and ultraviolet effects. They recognized the high transmission of vita glass in the infra-red. At the end of the paper they state that "the present investigation is hardly more than a limited survey" and that "for conclusive results each species tested would require further examination."

Regarding the interpretation of the differences found in plants under vita glass as compared with those under common glass it is evident that the authors attach great significance to slight differences in favor of vita glass, which have been obtained with small plant populations not grown under carefully controlled conditions and often not checked by repeated experiments. For instance, corn was planted on March 30 in flats under vita and common glass respectively. One month later eight plants from each flat were weighed and showed that percentage dry weights as compared with fresh weights were 7.5 and 6.7 respectively for vita and common glass. "There was therefore a somewhat greater yield of dry tissue under Vitaglass." "Tassels and silks appeared . . . two days earlier under Vitaglass than under common glass." At this time "to promote maturation the cultures were reduced to two plants, each . . . and received an application of KNO_3 ." Weights on parts of the two stems from each culture (the three internodes adjacent to the best ear) revealed greater weight for those under vita glass.

The most consistent "compositional response" to vita glass was an increased percentage of lipides in the dry matter. In five out of sixteen tests the ether extracts from plants under vita glass were either lower or no higher in lipides than were those under ordinary glass. The other eleven cases showed slightly higher percentages for plants under vita glass. In another paper (159) entitled "Are Leaf Lipides Responsive to Solar Radiation" a higher percentage of lipides for tomato plants under vita glass is again reported.

While these percentages are small, the fact that increases have been reported in a number of cases may indicate a vita glass effect. Certainly, however, from such experiments we are not justified in attributing this to effects of the region 290 to 310 $m\mu$. alone.

In England there have been numerous reports on plants grown under the English vita glass including those of Russell (122), the Kew Gardens (70), Saleeby (125), H— (60), Colman (27), Westfield College (1),

Maddock (81), Thomson (155), Graham and Stewart (57), Tincker (156) (157), Pilkington (103), and Secrett (132). In Germany results of experiments on plants grown under the various German glasses of this type have been made by Kache and others (69), Dix (40), Herold (63), Reinhold alone and with others (116, 117, 118), Roeder (119), Grossman (59) and one anonymous (3). A detailed review of these experiments is not necessary here inasmuch as the majority of them were ordinary greenhouse experiments without adequate controls and all of a very preliminary nature. As might be expected there is no general agreement among them as to the results obtained.

In Sweden Lamprecht (76) has carried out one of the most careful investigations of this type. He has compared plants grown under Helasan glass which transmits about 50 per cent of the solar radiation from 290 to 310 $m\mu$., a somewhat higher percentage of ultraviolet than vita glass transmits, but not as high a percentage as Uviol glass transmits. The plants were carefully handled and spaced and environmental conditions made as uniform as possible. Great care was taken to have the thickness of glass panes comparable in the test and control houses in order that the intensity of radiation reaching the plants should not vary because of this factor. Relatively large numbers of plants, never less than 40, under each condition in each test were used, and each series of experiments was repeated several times. The results were treated statistically and probable errors taken into account. Fresh weights and dry weight percentages were determined and various chemical analyses made.

Six series of carrots were run with 46 to 122 experimental plants used in each series. In no case did the use of Helasan glass result in significantly increased fresh weight, dry weight, or any change in chemical composition. One series of parsnips and one of radishes, both root crops, as were the carrots, gave similar results. Two series of lettuce plants gave no significant differences in fresh or dry weights due to the type of glass used, but indicated a definite trend in dry weights in favor of Helasan glass. Two series of spinach, also a crop with large leaves, gave results similar to those of lettuce.

The conclusion regarding the effect of the ultraviolet portion of the solar spectrum as revealed by these experiments was that there was the possibility of a certain small significance in the production of dry weight, but that definite establishment of this point could only come from much more carefully conducted experiments. For the practical horticulturist the author thought the glass to be of little value.

A review of the facts brought out by these reports in regard to evidence for ultraviolet effects by the use in greenhouses of special ultraviolet transmitting glasses reveals that out of 31 reports, unqualifiedly favorable results are reported in only 8 cases and the data for these are either not given or are of questionable value. The other articles report either conflicting results, results which could not be duplicated, very slightly favorable, or indifferent results. Of these at least 10 report the greater temperatures or heat effects under the special glasses. Several report more favorable results under them early in the spring, but not in the summer; a number report solarization effects of the glasses. The most carefully conducted experiments show nothing or very little in favor of the new glasses. Even were we to assume that all the beneficial effects reported were true, we should still have to hesitate to recommend the use of the special glasses for greenhouses because of the slight differences that have been found in even the most favorable reports.

Summary of the investigations dealing with general and specific effects of ultraviolet radiation upon more mature plants

Viewing as a whole the evidence presented in this large group of papers on the effects of ultraviolet on more mature plants, we observe that the only point which seems to be clearly demonstrated is that the short-wave ultraviolet, that from 289 to 200 $m\mu$. is distinctly harmful. Even in very slight doses it has never satisfactorily been demonstrated to be beneficial. The degree of injury increases with decrease of wave length, increase of intensity and with greater ease of penetration. While we would not overlook the possibility of beneficial effects being demonstrated for the longer wave-lengths when accurately controlled experiments are forthcoming, the evidence from the most accurately controlled experiments to date shows little if any outstanding beneficial effect of that region of ultraviolet present in sunlight, particularly the region 291 to 313 $m\mu$., which has been given much emphasis in animal and human physiology and has consequently been assumed by many to have beneficial effects on plants. Consequently we would not expect to find striking effects to be produced by this region in the future. It should be remembered that this region makes up a very small percentage of the total solar radiation reaching the earth. Certainly it has been demonstrated that many different kinds of plants can be grown from seed to seed in the total absence of all ultraviolet without exhibiting any very outstanding difference from plants receiving solar ultraviolet.

PART III

OTHER EFFECTS OF ULTRAVIOLET RADIATION UPON SEED PLANTS

Certain points relative to the significance of ultraviolet radiation which have not been mentioned in the preceding discussion will now be noted briefly.

The degree of penetration of ultraviolet radiation into plant cells

Of great importance with regard to the effect of ultraviolet radiation upon plants is the question of the degree of penetration of these rays into the various plant tissues, since only those rays which penetrate can be effective in producing results. Undoubtedly the facts that certain plants are more resistant than others to the harmful action of short rays, certain parts of a given plant more resistant than other parts of the same plant, and the same parts of a given plant more resistant at one stage of development than at another, owe their explanation in part at least to differences in degree of penetrability and absorption of these injurious rays. Different degrees of penetrability may also explain some of the conflicting results of past experiments. Thus the shorter lethal ultraviolet regions are ineffective if they strike plant parts opaque to them. Furthermore, any beneficial rays would have to enter the cells before they could be effective. Different media vary considerably in their capacity to transmit radiation of various wave lengths.

In earlier investigations the penetration of injurious rays only, was considered, and the degree of penetration was known only indirectly by the degree of injury produced on the plant cell as a result of irradiation. Maquenne and Demoussy (82), Kluyver (71, 72), and Ursprung and Blum (165) noted the superficial action of ultraviolet radiation of short wave lengths as indicated by the fact that only epidermal cells or those immediately beneath them were destroyed. They assumed that the harmful rays were absorbed by these external layers and failed to penetrate more deeply. Stoklasa (150) found that flowers were much more sensitive than leaves to short-wave ultraviolet, and that both leaves and flowers of hothouse plants were more sensitive than those of outdoor plants. Dangeard (32, 33) by noting various degrees of injury in different plants which had been irradiated assumed differences in degree of penetration of the harmful rays. He also thought that hairy leaves retarded penetration more than glaucous or smooth ones. Schroeter (130) thought that the thick cuticle of alpine plants protected them from the destructive action of the short wave lengths present in solar radiation. Köhler (75) using the cadmium line at 275 $m\mu$. showed that cuticularized, suberized, and lignified walls were not

penetrated by waves of this length and explained the greater resistance of some leaves to ultraviolet on the basis of differences in the degree of penetration of the harmful rays. Schulze (131) by photomicrographs also demonstrated that the cuticle, epidermis, and xylem absorb strongly in the region of 280 $m\mu$. while parenchyma, phloem, and young cambium are quite transparent to this region. He found strong absorption to occur in the middle lamella. He and Köhler showed that the nucleus absorbs strongly at wave-lengths 280 $m\mu$. and 275 $m\mu$. respectively. Dhéré and De Rogowski (39) found that pure chlorophyll was remarkably transparent to ultraviolet but that the natural chlorophylls in ether solution had a common absorption band near the middle of the ultraviolet spectrum, which would be at about wave length 304 $m\mu$.

More recently Bucholtz (20), Metzner (92), and Shull and Lemon (144) have published on this subject. Bucholtz noted that leaves of *Mnium* and the stamen hairs of *Tradescantia reflexa* were much more resistant to the lethal action of ultraviolet than bacteria and paramoecia, probably because of the greater opaqueness of the cells of higher plants. He used wave-lengths of the range 3654 to 2378 Å.

Metzner's work (92) was rather extensive. He used long wave ultraviolet (350–400 $m\mu$.) in his studies and his results were determined photomicrographically so that he had direct evidence of the actual penetration. He found that cellulose, hemicellulose and silicified walls were relatively transparent to this region. The plasma and nucleus absorbed weakly. On the other hand, corky and cutinized walls, and lignified ones to a lesser extent absorbed strongly in this region. Particularly strong absorption occurred in the cell sap of the epidermis, guard cells, and mesophyll of many plants; this absorption was thought to be due to the presence of tannins and flavones and to be of biological significance.

Of importance in relation to the effect of ultraviolet radiation upon seed germination is the paper by Shull and Lemon (144), which deals with the penetration of various seed coats by the radiation of an unscreened quartz mercury arc. Results were determined by spectrograms. They found that, with a maximum duration of irradiation of one hour, only the longer ultraviolet rays penetrated seed coats, the lowest limit being indicated by a feeble line at 312 $m\mu$. and penetration of rays shorter than 363 $m\mu$. always being feeble. There was some variability in penetration shown by different species. Even in the same seed coat there was variation. Thus in the case of corn grain membranes penetration was greatest on the embryo side. Wet coats differed little from dry ones as far as penetrability was concerned.

In this paper there is an actual demonstration of the reason mentioned

as a probability by Popp in 1921, for the failure of the short-wave ultraviolet to injure ungerminated seeds, namely, the failure of these rays to penetrate the seed coat. This paper also gives evidence which suggests that the region of ultraviolet used in Masure's investigation did actually penetrate the seed coats of his seeds.

It should be noted that no determinations of penetration to date have given percentage transmissions of various wave lengths through seed coats or any other plant parts. In other words, we have only qualitative and no quantitative data.

Effects of ultraviolet radiation upon anatomical structure

Since the penetration of the shorter ultraviolet rays is probably not very great, one would not expect them to have any considerable direct effect on the anatomical structure of plants except for the destructive action to the superficial cells. There is, of course, the possibility of chemical changes being brought about in the superficial layers which might in turn affect deeper lying cells, but we have no evidence for this. As for the longer more penetrating ultraviolet rays there is no evidence of their effectiveness in this field either.

Pfeiffer (102) reports that plants grown in daylight under Noviol "O" glass, which cuts off practically all ultraviolet, are less stocky, less sturdy, more watery, and weaker in vascular development than those grown under Corex glass which transmits all wave-lengths of solar ultraviolet.

From the fact that stem diameters, stem heights, fresh weights, dry weights, percentage of moisture and chemical analyses of plants grown under similar conditions by Popp (108) showed no marked differences we should not expect to find marked internal anatomical differences. Such differences were not found by Popp. The difficulty in obtaining sufficient and comparable material for anatomical study under such conditions renders anatomical differences found of doubtful significance unless they are very marked.

With the quartz mercury arc as a source of radiation Delf, Ritson, and Westbrook (37) have recorded as unscreened arc effects on leaves, in addition to the collapse and death of the epidermal cells, a decrease in thickness of the leaf, more compact mesophyll and palisade tissue and a reduction of mechanical tissue. Eltinge (43) in general has duplicated these results. Her anatomical data on plants screened either by vita glass or quartzlite glass indicate no outstanding effects for any given treatment.

Dane (30) has described unscreened arc effects on soybean stems. Irradiated plants had stem diameters one and one half times as large as the stems of controls. There was a reduction in the number of medullary rays.

Meristematic tissues remained active for a longer time in irradiated plants than in the controls. While the cells of the medullary rays under ordinary conditions remained parenchymatous, in irradiated plants they developed into xylem and phloem. Irradiated stems became hollow.

None of these experiments with artificial radiation were carefully enough controlled to warrant ascribing the effects noted for irradiated plants to ultraviolet alone.

The effect of ultraviolet radiation alone on anatomical structure is still largely to be determined.

The relation of ultraviolet radiation to the formation of chlorophyll and anthocyanin

While Stoklasa (150, 151) noted that exposures not exceeding two hours to wave lengths 300 to 500 $m\mu$. of a mercury arc generally caused a rapid development of chlorophyll in etiolated plants, and that etiolated plants exposed to this region of sunlight became green more rapidly than those exposed to full sunlight, Dangeard (31) claimed that blue and violet light from a Nernst lamp seemed to have little influence on chlorophyll synthesis, and that the energy absorbed below 490 $m\mu$. was insufficient to bring it about. Sayre (126) has said that with sufficient energy value chlorophyll develops in that region of the ultraviolet between 300 and 400 $m\mu$. In many reports a deeper green color of plants under one of the special ultraviolet transmitting glasses has been reported, but it should be noted that this is not necessarily an indication of greater chlorophyll development, as this appearance may be brought about by a more compact tissue, a broken down epidermal layer, lack of hairiness, etc. In addition, as has been indicated before, effects under these special glasses are not necessarily ultraviolet effects. Colla (28) found that chlorophyll developed in plants exposed to radiation of wave-lengths 330–390 $m\mu$. the amount being comparable to that produced in ordinary light of low intensity. In none of these cases has there been quantitative determination of chlorophyll.

Shirley (143) determined quantitatively the amount of chlorophyll developed using the method of Willstätter and Stoll as modified by Shertz. Plants grown under a blue glass transmitting the region between 374 and 585 $m\mu$. under 10 per cent of the total intensity of daylight often gave a higher concentration of chlorophyll than any other light qualities used under the same intensity. At the same time the chlorophyll concentration was usually lower under G34 glass which transmits no radiations shorter than 529 $m\mu$. He found that "in all light qualities used the plants increased their chlorophyll concentration with decreasing intensity to a certain point." When plants from which only the ultraviolet was removed under

65 per cent of the total intensity, were compared with those receiving the full spectrum of daylight under 68 per cent intensity, no significant difference in chlorophyll content was found in *Geum*, sunflower, or *Galinsoga*. This is the only investigation in which quantitative determinations of chlorophyll were made under various light qualities.

A relationship between ultraviolet radiation and the development or presence of anthocyanin and related compounds in plant cells has been suggested in a number of cases. Shibata, Nagai and Kishida (139, 140, 141, 142) found that the cell sap of epidermal and peripheral parenchymatous cells of the aerial parts of plants in general, commonly contained flavone derivatives. Furthermore, according to them, these compounds were limited almost exclusively to these parts of plants. They also noted that plants in sunny habitats contained greater amounts of flavones than those in shady places, and that alpine plants were richer in flavones than those in lower regions where the intensity of solar radiation was not as great as in alpine regions. In general plants exposed to intense sunlight showed a greater development of flavones than those under lower intensities unless the plants were protected by some morphological feature such as a thick cuticle. Thus *Ficus elastica*, a tropical plant grown under strong light intensity had leaves with a low amount of flavones, but these leaves had a thick cuticle. Rosenheim (120) thought that if the findings of Shibata, Nagai and Kishida were true, then alpine plants grown at lower altitudes should not contain as much flavone as those grown in alpine regions. Using *Edehweiss* as an example he found that this plant actually did not develop as much flavone when grown at lower altitudes as when grown in the Alps.

Schanz (128) noted that much of the red color of red-leaved lettuce grown outdoors disappeared when the plants were placed under ordinary window glass which cut off most of the radiation below 320 $m\mu$., while all of it disappeared if wave lengths shorter than 388 $m\mu$. were eliminated. When young plants of *Celosia Thompsoni* with dark red leaves were placed in daylight under various screens the new leaves which formed were less red and more green the more the short wave lengths were eliminated, and were completely green when wave lengths shorter than 420 $m\mu$. were removed. Red beet leaves lost the red color in the absence of ultraviolet radiation, but the stems and petioles remained red.

These investigators have all attributed possible biological significance to the development and presence of these anthocyanins and flavones. One of the possible rôles suggested for these substances was that they absorb ultraviolet radiation and consequently protect deeper lying cells from its injurious effects. Metzner (92) has demonstrated that strong absorption of the region 350 to 400 $m\mu$. occurs in cell sap which contains tannins and

flavones. However, this hypothesis loses weight when it is remembered that ultraviolet radiation of the intensity and quality present in solar radiation has never been conclusively demonstrated to be injurious to plants. Such evidence as is available, as for example that of Arthur and Newell (8), indicates rather that ultraviolet of the intensity and quality present in daylight is not injurious.

One of the possible demonstrations of the injurious effects of solar ultraviolet is indicated by Schanz's experiment with the purple beech (128). While the experiment was not carried out with proper controls it does indicate a possible destructive action of short wave radiation on plants containing epidermal anthocyanin when they are first grown under conditions which prevent the development of this anthocyanin and later exposed to radiation containing ultraviolet. Schanz, having raised this purple beech under various screens, found that it lost its red anthocyanin color the more the short waves were cut off. He then transplanted one of the plants which had developed large green leaves lacking anthocyanin to the open where it was exposed to the full radiation of daylight. At the end of 14 days all of these green leaves were dead and the new ones that had developed were red in color. Schanz concluded that possibly the red anthocyanin acted as a screen here to protect the plants against ultraviolet radiation. Unfortunately plants that had already developed anthocyanin were not transplanted to the open in a similar manner. Furthermore, other species of plants containing a similar anthocyanin relationship were not injured when placed in the open. This situation might be cleared up if such plants as the purple beech were first grown under conditions in which anthocyanin fails to develop and then exposed to an artificial source of ultraviolet by the same method as was used by Arthur and Newell. Then at least we would be able to ascertain whether such plants were more sensitive to long-wavelength ultraviolet than ordinary plants.

Arthur (7) was able to bring about the development of red pigment in McIntosh apples by irradiating them with a mercury vapor arc in Uviol glass at a distance great enough to prevent injury. Forty hours exposure was necessary to cause this coloration in apples gathered August 25, but the period increased with increase in age of the apple after August 27, and with time of storage. No pigment developed in fruits taken from storage in January. Peelings of apples floating upon water and irradiated developed color similarly, but those killed by heat or alcohol and then irradiated, developed no red color.

A recent note from the New York State Agricultural Experiment Station (4), states that McIntosh apples that had shown no red color originally, became completely red when exposed for 4 or 5 days to a 1500 watt

electric lamp. This would indicate the possibility that other wave-lengths besides ultraviolet may be effective.

While ultraviolet radiation may affect the development of anthocyanin it is definitely known that such radiation is not absolutely necessary for all anthocyanin formation. Popp (106, 107) for instance found that mustard seedlings grown continuously in the dark or grown in the dark and exposed to the mercury arc from which the ultraviolet portion had been eliminated, formed anthocyanin. The fact that beet roots developed in the soil in the absence of all radiation are rich in anthocyanin is well known. That anthocyanin formation is favored by ultraviolet radiation is possibly indicated, however, by experiments such as those just referred to, although ultraviolet effects have never been clearly separated from total radiation intensity or from blue-visible effects.

The effect of ultraviolet radiation upon cell contents

The nature of the influence of ultraviolet rays on the cell contents themselves has been investigated more intensively in the cells of lower plants and animals than in those of higher plants. There is no doubt that the reaction of protoplasm to such irradiation is complex. No attempt will be made in this report to go into the details of such reaction. In general investigations such as those of Downes and Blunt (41, 42), Burge (21, 22), Harris and Hoyt (62), Bovie (18, 19), Barr and Bovie (12), Gates (52, 53, 54), and others have indicated that short wave ultraviolet (below 290 $m\mu$.) causes a cytolysis in lower organisms. Gates found that wave lengths 260 to 270 $m\mu$. produced the maximum bactericidal action, which is contrary to the general findings indicating that the shorter the wave length the greater the bactericidal action. The coagulation of the protoplasm is a prominent factor in this cytolysis. Studies in vitro have demonstrated the coagulation of proteins by ultraviolet radiation. The killing effects of the radiation of an unscreened mercury arc upon the superficial cells of higher plants have been noted by every investigator who has examined such cells, including Maquenne and Demoussy (82), Schroeter (130), Schulze (131), Kluyver (71, 72), Stoklasa (150, 151, 153), Ursprung and Blum (165), Sibilia (145), Delf, Ritson, and Westbrook (37), Martin and Westbrook (86), Nadson and Rochlin (96), Bucholtz (20), and Popp and Brown (109, 110).

Protoplasmic streaming of irradiated cells has been noted in a number of cases. In general the first reaction is a stimulation or increase in the rate of streaming which reaches a maximum, decreases, and finally ceases, the cessation marking the beginning of necrosis of the protoplast. Hertel (64, 65) and Schulze (131) have recorded the retardation and final cessa-

tion of protoplasmic streaming of *Elodea* leaf cells and certain other plant parts under monochromatic radiation of wave-lengths near 275 m μ . and 280 m μ . More recently Noethlin and Rochlin (97) in rather extensive experiments have shown that short wave ultraviolet is more effective than all other regions of the spectrum of a mercury vapor arc in inducing plasma streaming. The elimination of the infra-red by a water screen did not affect the results. They explain Nothmann-Zuckerlandl's (98) failure to observe plasma streaming under the influence of the shorter visible and ultraviolet as due to the fact that the cells were not observed closely after irradiation and that they were killed so rapidly that they showed no great visible differences from living cells when finally observed.

There is evidence that ultraviolet radiation may promote oxidation phenomena. Nadson and Rochlin (95, 96) have thought that this causes among other things the transformation of starch grains into calcium oxalate crystals with sugar probably as an intermediate product. They have illustrated photographically what they thought to be the various visible stages in this transformation. Beauverie and Cornet (13) have thought that ultraviolet radiation produces hydrogen peroxide in the medium which causes a kind of fixation in the structure of the cells of leaves and buds of *Elodea canadensis*. This hypothesis was strengthened by the direct action of hydrogen peroxide used in some experiments. The investigation was to be continued on aerial organs to eliminate the possibility of the intervention of products formed in the medium.

Ultraviolet radiation has been shown to interfere with cell division. Schulze ('31) found that the magnesium line at 280 m μ . retarded cell division in *Tradescantia*. Takamine (154) noted the effect of the line 250 m μ . of a mercury arc at distances of ten to twenty centimeters for periods of one half to three hours on the root tips of *Vicia faba*, *Allium cepa*, the pollen mother cells of *Capsella bursa pastoris*, *Lactuca thunbergiana*, and *L. lanceolata platyphylla*. He noted various irregularities including the stricture and breaking up of chromosomes, irregular distribution of chromosomes, and sometimes tripolar divisions of somatic nuclei. In pollen formation not all tetrad cells developed into grains; some disintegrated.

Lepeschkin (78) noted that the rays most active in influencing changes in the permeability of protoplasm were those transmitted through a G586A Corning filter, that is the region 320 to 420 m μ ., with a maximum at about 370 m μ .

Short wave ultraviolet in general has been found to weaken or destroy enzyme activity. Green (58) and Hertel (64) reported the weakening of diastase activity, Green using ultraviolet and blue rays, and Hertel monochromatic wave length of 280 m μ . Chauchard and Mazoué (25) and Agul-

hon (5) also report the destruction of enzymes by ultraviolet. Burge, Fischer, and Neill (23) found that pepsin, trypsin, enterokinase, ptyalin, amylopsin, and the proenzyme trypsinogen were all destroyed by ultraviolet radiation. The destruction of enzymes by ultraviolet radiation has led some to believe that ultraviolet kills living cells by destroying the enzymes within them. Burge, however, (21, 22) has demonstrated that ultraviolet may kill bacteria without destroying the intracellular proteolytic enzymes. In these tests he used bacteria which by virtue of the proteolytic enzymes within their cells possess the property of liquifying gelatin. He killed such bacteria by exposure to ultraviolet radiation, ground them up, after centrifuging, with sand and 30 per cent alcohol to extract the enzyme, and found that the treatment had affected the enzymes but slightly since the results of their activity on gelatin were very little different from the results obtained with living bacteria. He concluded that the death of the cells was due to the coagulation of the protoplasm, brought about by the radiation. Fuller (51) reported at the New Orleans meeting of the Botanical Society that catalase and diastase activity were increased in plants exposed to the lethal ultraviolet region. As our only means of detecting enzyme activity is by measuring the end products of its action results may indicate increased action in irradiated plants for several reasons. It may happen that enzymes formerly confined to certain cells are liberated as a result of irradiation and brought into contact with the proper substrate for activity. Maquenne and Demoussy (83, 84, 85) have emphasized that the blackening of leaves is considered as due not to the specific action of ultraviolet rays, but as a result of diastatic or other enzyme activity brought about by the liberation of enzymes formerly confined within certain cells. Evidence in favor of this view was that blackening could be produced by any means which would destroy the protoplasm such as mechanical injury, chloroform, heat, etc. Paine (101) has confirmed the results of Maquenne and Demoussy. Pougnet (112, 113) has called attention to the fact that various odors which are developed from plants under a mercury vapor arc are caused by the splitting of glucosides. This was thought to occur because of changes of permeability of the protoplasts caused by the irradiation which allowed the interaction of enzyme and glucoside, formerly separated from each other. Ultraviolet radiation may also have a direct effect upon the substrates themselves or upon plants without the intervention of any enzyme activity and result in increased quantities of end products which may be similar to those produced by the action of enzymes. Thus Bierry, Henri, and Ranc (15, 16), Euler and Ohlsen (45), and Berthelot and Gaudechon (14) have shown the inversion of saccharose and other sugars by ultraviolet radiation in the absence of enzymes. The whole subject requires further investigation.

Miscellaneous effects of ultraviolet radiation

Studies with ultraviolet radiation have played a prominent part in recent years in vitamin work. Most of the studies, however, have been conducted with animals. In some cases vitamin formation in plants has been attempted by exposing them to ultraviolet radiation, but the ultimate aim of these investigations was to secure vitamins to feed to animals. No attempt will be made in this discussion to review the papers in this field, but the work of Lojkin (79) will serve as an illustration of this type of study. She has made an extensive investigation on certain effects of ultraviolet rays on the vitamin D content of plants as compared with the direct irradiation of the animal. The vitamin D, whether formed in the plant or in the animal, is thought to be due to the activation of ergosterol. Previous experiments by various workers such as Hess and Weinstock, and Steenbock and Black had yielded conflicting results as to the antirachitic properties possessed by various plants. In the experiments of this investigation lettuce, alfalfa, spinach, New Zealand spinach, and soy beans developed a slight potency in solar radiation under a special ultraviolet transmitting glass. Neither these, nor cabbage nor swiss chard produced vitamin D under ordinary glass. Irradiation of plants by a mercury arc gave considerable potency except for cabbage, 30 minute exposures being optimum. Cut plants were more potent than those left attached to the roots during irradiation. The minimum exposure necessary to produce an appreciable amount of vitamin D in plant tissues was found to be considerably longer than that required to impart complete protection by direct irradiation of the animal. Even with filters of comparatively low transmission in the extreme ultraviolet (lower limit 286 m μ .) an irradiation of one minute of the animal gave complete protection. The shorter ultraviolet rays not present in sunlight were said to be of little value in protecting against rickets, probably because of their failure to penetrate into the cells containing the ergosterol. With a sunlight source, 30 minutes per day in winter and 15 minutes in summer protected rats if they were not given a diet which made them grow too fast, under which conditions the more rapid formation of bone tissue made longer exposures necessary. From these experiments it would seem that from a practical standpoint the direct irradiation of the animal was far more efficient than the irradiation of plants later fed to the animal in supplying the animal with a sufficient amount of vitamin D.

The significance to the plant itself of vitamin formation or of the presence of vitamins in plants has not been determined.

A discussion of the relation of ultraviolet radiation to the synthesis of carbohydrates and proteins is beyond the scope of this paper. The reader

is referred to papers such as those of Tolomei (158), Stoklasa (152), Laurent and Marchal (77), and Ursprung (163) for indications of syntheses occurring in plants under ultraviolet radiation or to those of Kniep and Minder (74), Ursprung (164), Warburg (167), Warburg and Negelein (168), and Schmucker (129) for reports on the relative efficiency of various wave lengths for photosynthesis. More references and a discussion of the relation of ultraviolet to photosynthesis can be found in the excellent monographs on photosynthesis by Stiles (149) and by Spoehr (148). A brief summary of this subject may be found in "The Chemistry of Plant Products" by Haas and Hill (61).

Since the time of Sachs (124) and DeCandolle (34) ultraviolet has been said to influence favorably flower formation. Eltinge, Ballan, Westfield College reports, Michigan Station reports, and Tottingham and Moore have all suggested earlier or better flowering in certain cases as an ultraviolet effect, but it has already been noted that such effects were not consistently obtained and were usually associated with temperature or other differences when comparisons were made with control plants. Popp found that elimination of practically all ultraviolet had no effect on the time or amount of flowering of many of his plants. In some cases the earlier flowering plants were those from which practically all ultraviolet was screened off.

That the injurious effects of ultraviolet radiation are only temporary has been emphasized by Sibilia (145), Jacobi (68), Popp and Brown (110) Arthur and Newell (8), and Detwiler (38) who found that temporary effects on general appearance, color, size, general vigor, and weight disappeared when the injurious irradiations ceased, the length of time necessary for this being dependent upon the degree of injury, unless the injury was too severe, in which case the plants died. McCrea (88, 89, 90, 91) found what she thought to be a lasting physiological effect in the greater production of digitalin in *Digitalis purpurea* months after the test plants with the controls had been put outdoors.

The fluorescence of seeds germinating under irradiation by the region 300 to 400 $m\mu$. has been noted by Gentner (56), Mezzadrolì and Vareton (94), Foy (47), and Masure (87), but its significance is not known. Gentner has attempted to find out whether the nature of the fluorescence is specific enough that it may be used practically for seed testing, particularly for the differentiation between seed varieties and races. Foy has used this method successfully in diagnosing various types of rye-grass in New Zealand. The annual Italian rye-grass and some or all of the false perennial types exhibit a brilliant blue fluorescence while the true, normal, perennial rye-grass reacts absolutely negatively.

The relation of ultraviolet radiation to transpiration (43), respiration (87), sunscald (80), winter hardening (161), tropisms (46), electric potentials and currents in plants (138) and to various other miscellaneous effects ascribed to it will not be discussed because the evidence is too fragmentary.

CONCLUDING REMARKS

In spite of the many publications on the subject, exact knowledge regarding the influence of ultraviolet radiation upon seed plants other than its destructive action is still to be ascertained. The interest in ultraviolet in recent years has been so widespread as to justify the accusation of some that the subject is a fad. It is to be hoped that the "fad" will not run its course before accurate information has been obtained. Needless to say, such information will not be forthcoming from experiments of short duration, carried out with a few plants under poorly controlled conditions such as have predominated in the work of the past.

Much of the present uncertainty of our knowledge of the effects of radiation upon plants rests upon the complexity of the problem itself. No other environmental factor is so variable or so difficult to control. The fact that plants require visible radiation for normal growth necessitates supplying them with this radiation. Sources of visible radiation usually contain also infra-red radiation. Consequently these factors must be considered and equalized in test cultures and controls when the effects of ultraviolet are to be studied. Total radiation measurements, transmissions of screens, spectrograms of the radiation used, and the like, are in themselves insufficient to give a complete picture of the nature of the radiation reaching plants, although in many papers, even these variables are not given. Few, if any, authors have measured the total energy or the distribution of the energy in the ultraviolet to which results were attributed, to say nothing of the failure to equalize the radiant energy of other wave lengths reaching the test plants as compared with the controls. While it is conceded that these measurements are difficult to make, it must also be admitted that so long as they remain unknown in an experiment the results cannot be attributed to ultraviolet any more than to any other operating variable.

In addition to the necessity of having a complete description of the radiation reaching plants it is no less important to know whether the plants or plant parts studied absorb selectively different portions of the spectrum and to what extent. Possible photochemical reactions in the plant may be greatly accelerated in a relatively narrow region of the spectrum that is strongly absorbed, whereas comparatively high intensities in a region that is feebly or not at all absorbed might be without effect.

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The rate of fall of spores in relation to the epidemiology of black stem rust¹

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(WITH FOUR TEXT FIGURES)

INTRODUCTION

The periodic occurrence of epidemics of stem rust in the spring-wheat area has led to investigations of the probable factors involved in their development. Obviously, two of the primary requisites for the development of epidemics are abundant inoculum and some means for its general dissemination. Air currents and high winds are known to play an important rôle in the dissemination of some fungus spores. That they are important also in the dissemination of cereal rusts is generally accepted.

Stakman, Levine, and Wallace (1929) give three possible sources of stem-rust inoculum for the spring wheat area: urediniospores that survive the winter in the North; acciospores from barberry bushes; and wind-borne urediniospores from the South. The possibility that cereal rusts that develop in early spring in Mexico and Southern United States serve as inoculum for the northern areas presupposes the long-distance dissemination of spores. Inoculum from the South could migrate in two ways, either by successive northward migration for comparatively short distances or by a continuous journey from the infected areas in the South to the grain fields in the North.

Lambert (1929) discussed the evidence of long-distance dissemination of spores and was of the opinion that under favorable atmospheric conditions stem rust urediniospores could be carried from Texas to the spring-wheat area in three days.

Stakman, Levine, and Wallace (1929) and Wallace (1932) concluded from a comparison of the physiologic forms of stem rust present in the South and the North that very little rust was blown northward in 1926, but that in 1927 and possibly in 1928 a migration of rust occurred. Stakman *et al.* (1923) demonstrated by slide exposures from airplanes that rust spores often reach high altitudes. Urediniospores of *Puccinia graminis* Pers. and *P. triticina* Eriks., as well as spores of other fungi, were found to be fairly common at altitudes up to 10,000 feet.

From these investigations it seems clear that spores may often reach high altitudes and that they probably are carried long distances by favor-

¹ Cooperative investigations by the Division of Barberry Eradication, Bureau of Plant Industry, U. S. Department of Agriculture, and the Agricultural Experiment Station of the University of Minnesota. Paper No. 1135 of the Journal Series of the Minnesota Agricultural Experiment Station.

able winds. Obviously, the rate of spore fall is one factor determining how far they can be carried by the wind. For this reason the studies reported in this paper were made.

The distance spores can be carried by air currents will depend upon three factors: the altitude attained by the spores, their rate of fall in air, and velocity and duration of winds. As spores have a large surface area in proportion to their mass they would fall at a relatively slow rate.

Buller (1909) determined microscopically the rate of fall of basidiospores of some of the Hymenomycetes by means of a specially constructed apparatus consisting of a compressor cell fitted to a horizontal microscope. A small piece of the fruiting body of the fungus was placed in such position that the spores, when liberated, fell vertically across the microscopic field. Fine silk threads were attached to the eyepiece in such manner as to mark off a distance of 4.55 millimeters. The time required for the spores to fall across that part of the microscopic field delimited by the silk thread was determined. It was found that spores of different species fall at different rates, ranging from 0.49 mm. per second in the case of *Collybia dryophila* Fr. to 4.29 mm. per second for *Coprinus plicatilis* Fr. In general, the rate of fall increased directly with the size of the spores, although this was not true in all cases.

McCubbin (1918) determined the rate of fall of air-dried urediniospores of *Cronartium ribicola* Fisher. The spores were released at the top of an 8-ft. cardboard tube and caught on slides placed at the bottom. It was found that urediniospores continued to fall on the slides over a period of 5 minutes. On the first slides exposed after the spores were released, many irregularities were noted, due to the falling of clumps of spores. Spores requiring 5 minutes to fall 8 ft. would fall at the rate of approximately 8 mm. per second.

The rate of fall of urediniospores and aeciospores of *P. graminis* has never been determined. Because of its bearing on the dissemination of cereal rusts by air currents, the rate of fall in still air of spores of four different cereal rusts was studied.

Field observations on the development of rusts indicated that *P. graminis* and *P. triticea* are disseminated over large areas in most years. *P. coronata* Corda, however, although usually abundant in the southern states, seems to migrate northward less frequently. A difference in the rate of fall of spores of different species might account in part for this apparent difference in dissemination.

MATERIALS AND METHODS

The rate of fall of urediniospores was measured in a galvanized-iron cylinder 6 ft. long and 6 in. in diameter (fig. 1). The lower end was closed

and the upper end covered with a tight-fitting lid. Three sides of the cylinder near the lower end were fitted with glass windows $2\frac{1}{2}$ in. \times 5 in., the lower edge of the windows being 3 in. from the bottom. At the bottom of the cylinder two openings $1\frac{1}{4}$ in. \times $\frac{1}{4}$ in. were cut on opposite sides, while a hole $\frac{1}{4}$ in. in diameter was made $\frac{3}{4}$ in. from the top. A small insect-powder gun was used to discharge the spores into the cylinder through the small hole in the upper end. This method of liberating the spores aided in breaking up spore clusters and resulted in the fall of a maximum number of single spores.

The spores were caught on glass slides covered with a thin film of vaseline and held by a wooden lath approximately 17 in. long and $1\frac{1}{8}$ in. wide. Two grooves, slightly larger than the glass slides, cut in the upper side of the lath held the slide in position. This lath was inserted through the openings at the bottom of the cylinder, passing directly through its center and protruding several inches on each side. The lath, when in position, held a slide placed in one of the grooves directly in the center of the tube. A second slide was inserted in the other groove on the outside of the cylinder. After the slide in the tube had been exposed the proper interval, the lath was drawn quickly in one direction to bring the exposed slide to the outside of the cylinder and, at the same time, to carry a fresh slide into the center.

A beam of light from a projection lantern directed through the glass windows made it possible to observe the fall of the spores. By watching the movement of dust particles in the air within the cylinder it was possible to determine the time when convection currents were almost absent

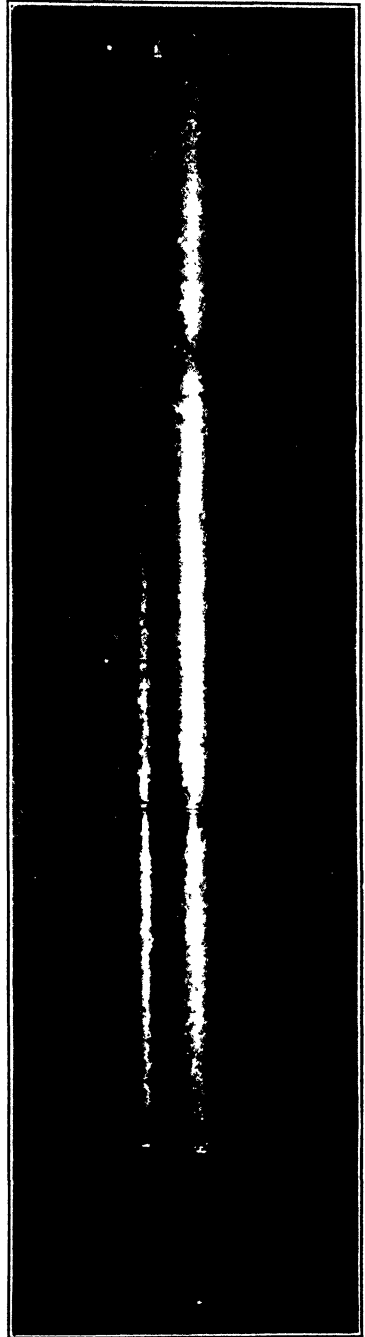


Fig. 1. Galvanized-iron cylinder used in measuring the rate of fall of urediniospores.

and therefore the most suitable time at which to release the spores.

Before each trial the cylinder was carefully washed with water to remove all spores present, after which it was dried over a radiator for a short time and then allowed to cool uniformly to room temperature.

The urediniospores used in the experiment were secured from stock cultures and increased upon suitable seedling plants. Only spores from well-developed pustules were used; they were removed by gently scraping the pustule with a small, rigid spatula. In all cases the spores were air dried for one hour before a test was made. A check slide was exposed for one minute in the cylinder at the beginning of each trial to determine whether the air was free of spores. In no case were any spores caught on check slides.

Slides were changed every 30 seconds from the time the spores were released until no spores were observed falling at the bottom of the cylinder. The entire surface of each slide was examined under low power of a microscope and the number of spores and clumps of spores caught during each 30-second period recorded.

The distance from the point of release at the top of the cylinder to the surface of the slide at the bottom was 180 centimeters; therefore, all spores caught on the slides fell this distance.

The galvanized iron cylinder was found unsatisfactory in measuring the rate of fall of aeciospores because of the difficulty encountered in liberating spores from the aecial cups. Accordingly, a method was devised by which the spores were liberated under more natural conditions.

The special apparatus used (fig. 2) consisted of a glass cylinder approximately 2 ft. long and $1\frac{7}{8}$ in. in diameter, a projection lantern to furnish sufficient light, and a microscope mirror to reflect the light upward through the long axis of the cylinder. The bottom of the cylinder was closed by covering with a circular piece of glass somewhat larger than the mouth of the tube and sealed with a mixture of beeswax and paraffin. This bottom could be removed for cleaning simply by melting the paraffin. The cylinder was held in a vertical position by means of a clamp attached to a ring stand. The microscope reflector was fastened directly under and 8 in. below the bottom of the cylinder. At the top of the cylinder was an opening $\frac{1}{2}$ in. in diameter through which the spore material was inserted. This opening was closed with a tight-fitting cork when the trials were being made. To a small glass rod extending through the cork and into the cylinder was fastened a small piece of blotting paper. Freshly cut barberry leaves with well developed aecia of stem rust were attached to this blotting paper, which was moistened at the beginning of each trial.

Under the conditions provided by the above described apparatus the

spores were shot from the aecial cups in large numbers. The reflector below the cylinder was tilted at an angle, and when light from the projection lantern was focused on it a beam was thrown upward through the full length of the cylinder. In this beam of light the falling spores could easily be observed. In order to eliminate the possibility of air currents being set up in the cylinder by heat from the projection lantern, a water bath was

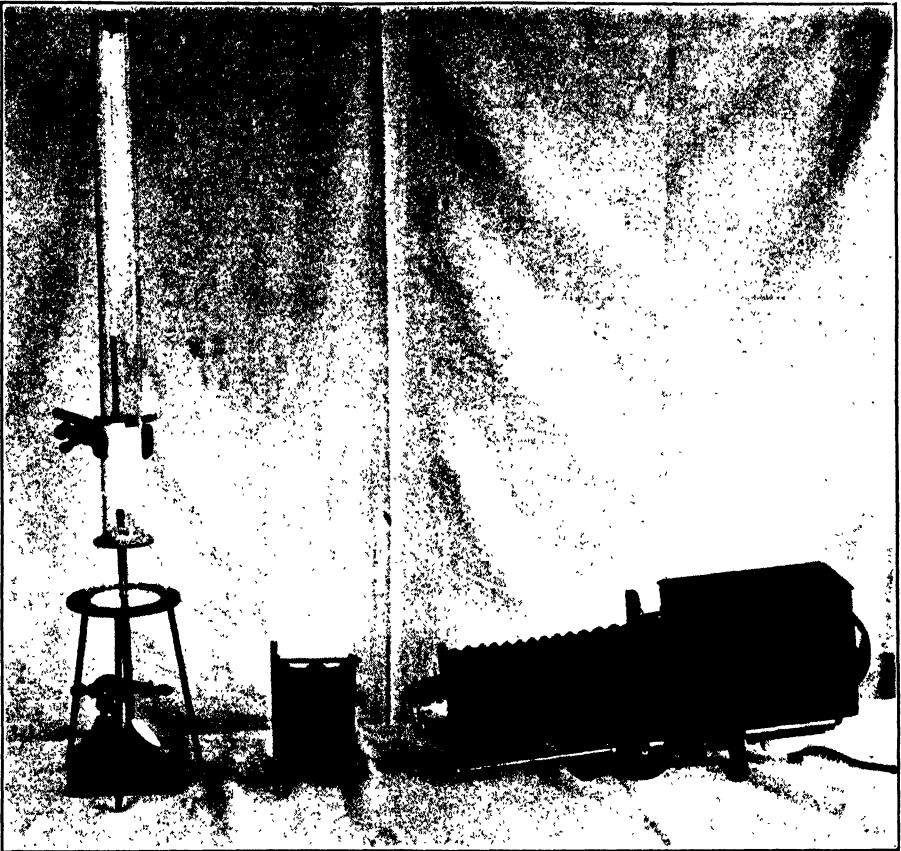


Fig. 2. Apparatus used in measuring rate of fall of aeciospores.

placed between the projection lantern and the reflector. A Petri dish filled with water and placed between the reflector and the bottom of the cylinder provided further for the elimination of heat.

A distance of 30 cm. was measured off on the cylinder and marked with a wax pencil, the upper mark being 3 in. below the infected leaves. The time required for the aeciospores to fall the distance between the marks on the cylinder was observed and recorded by a stop watch. The procedure was as follows: An infected barberry leaf was fastened to the blotting pa-

per, which, after being moistened, was inserted into the upright cylinder, with accia facing downward. In a short time ejection of acciospores began and they slowly fell to the bottom of the cylinder, their course being easily followed in the beam of light. Single spores were selected at random and their passage between the 30-cm. marks on the cylinder timed with the stop watch and recorded to the nearest second. Often large numbers of acciospores were ejected almost simultaneously and fell at a uniform rate more or less as a cloud. One spore from such a group was traced in its fall through the cylinder. After a little experience, no difficulty was encountered in following with the eye the fall of each spore selected.

RATE OF FALL OF UREDINIOSPORES

The rate of fall of urediniospores of *Puccinia graminis tritici* Eriks. and Henn., *P. graminis secalis* Eriks. and Henn., *P. coronata avenae* (Cda.) Eriks. and Henn., and *P. tritricina* was determined. Ten separate trials were made with spores of *P. graminis tritici*, while five tests were made with the other rusts.

The first spores to fall the length of the cylinder were in clusters, each cluster containing various numbers of spores. All having more than five spores were placed in one class because of the difficulty of determining the exact number, while clusters with five spores or fewer were classified according to the number of spores in each. Table 1 shows the total number of single spores and the number and magnitude of spore clusters of *P.*

TABLE 1

Number of individual urediniospores and spore clusters of Puccinia graminis tritici deposited 180 cm. from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

[illegible]

graminis tritici deposited on slides during the various periods of exposure. Clusters of spores fell with greater velocity than individual spores and, as the number of spores in a cluster increased, their average rate of fall also increased. Of the large clusters having more than five spores each, 94.5 per cent reached the slides $1\frac{1}{2}$ minutes after they were liberated (Table 2), while in that time only 0.7 per cent of the single spores were caught.

TABLE 2

Percentage of individual urediniospores and spore clusters of Puccinia graminis tritici deposited 180 cm from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

MAGNITUDE OF SPORE CLUSTER	EXPOSURE PERIODS (NO. OF SECONDS AFTER SPORES WERE LIBERATED)												TOTAL
	0- 30	30- 60	60- 90	90- 120	120- 150	150- 180	180- 210	210- 240	240- 270	270- 300	300- 330	330- 360	
	PERCENTAGE OF SINGLE UREDINIOSPORES AND SPORE CLUSTERS DEPOSITED ON SLIDE												
Individual spores	0	0	7.0	19.6	32.6	24.1	11.5	6.6	2.8	1.4	0.5	0.2	100
Clusters of 2 spores	0	0.6	15.0	46.6	29.5	7.9	0.4	0	0	0	0	0	100
Clusters of 3 spores	0	1.8	42.9	39.9	12.9	2.5	0	0	0	0	0	0	100
Clusters of 4 spores	0	2.6	67.1	23.7	6.6	0	0	0	0	0	0	0	100
Clusters of 5 spores	0	7.7	73.1	19.2	0	0	0	0	0	0	0	0	100
Clusters of more than 5 spores	0.7	45.9	47.9	5.5	0	0	0	0	0	0	0	0	100

The rate of fall of spore clusters is of minor importance from the standpoint of wind dissemination. Although spores may leave pustules in groups, they probably soon become separated under natural conditions. It is only the spores that reach high altitudes that would be important from the standpoint of long-distance dissemination, and, according to the results of slide exposures, individual spores are most likely to be carried to great heights. Although spores caught on slides exposed from airplanes have been found occasionally in groups of two or three, the majority caught at high altitudes have been individual spores.

Great variation was found in the time required for single urediniospores to fall the length of the cylinder. This was true in the case of all rusts with which tests were made. Some variation occurred in the different trials, due probably to slightly different conditions at the time of each test. Although no trials were made when air currents were noticeably present in the cylinder, it is quite possible they were not eliminated entirely and affected to a slight extent the rate of fall. The number of trials made, however, probably overcame the irregularity of any one trial.

A few spores of *P. graminis tritici* fell 180 cm. in $1\frac{1}{2}$ minutes, while other spores required 6 minutes to fall that distance. The largest deposit of spores on any slide occurred during the period from 2 to $2\frac{1}{2}$ minutes after liberation. This was true also in the case of *P. graminis secalis* and *P. triticea*, while the largest deposit of spores of *P. coronata* occurred during the next period, or from $2\frac{1}{2}$ to 3 minutes after liberation. Summaries of the totals obtained for the four rusts during each exposure period are given on a numerical basis in table 3, on a percentage basis in table 4, and shown graphically in figure 1.

TABLE 3

Number of urediniospores of four different cereal rusts deposited 180 cm. from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

RUSTS	EXPOSURE PERIODS (NO. SECONDS AFTER SPORES WERE LIBERATED)														TOTAL
	0-30	30-60	60-90	90-120	120-150	150-180	180-210	210-240	240-270	270-300	300-330	330-360	360-390	390-420	
	NUMBER OF UREDINIOSPORES DEPOSITED ON SLIDES														
<i>Puccinia graminis tritici</i>	0	0	34	1004	1669	1234	588	340	144	74	27	8	0	0	5122
<i>P. graminis secalis</i>	1	3	88	424	637	522	419	245	134	112	54	27	4	0	2670
<i>P. coronata</i>	0	0	22	190	805	1317	977	355	166	108	71	35	10	6	4062
<i>P. triticea</i>	0	0	44	490	517	169	97	77	37	19	13	5	0	0	1468

TABLE 4

Percentage of urediniospores of four different cereal rusts deposited 180 cm. from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

RUSTS	EXPOSURE PERIODS (NO. SECONDS AFTER SPORES WERE LIBERATED)														TOTAL
	0-30	30-60	60-90	90-120	120-150	150-180	180-210	210-240	240-270	270-300	300-330	330-360	360-390	390-420	
	PERCENTAGE OF UREDINIOSPORES DEPOSITED ON SLIDES														
<i>Puccinia graminis tritici</i>	0	0	0.7	19.6	32.6	24.1	11.5	6.6	2.8	1.4	0.5	0.2	0	0	100
<i>P. graminis secalis</i>	+	0.1	3.3	15.9	23.9	19.5	15.7	9.2	5.0	4.2	2.0	1.0	0.2	0	100
<i>P. coronata</i>	0	0	0.5	4.7	19.8	32.4	24.1	8.7	4.1	2.7	1.8	0.9	0.2	0.1	100
<i>P. triticea</i>	0	0	3.0	33.4	35.2	11.5	6.6	5.2	2.5	1.3	1.0	0.3	0	0	100

A comparison of results with the different rusts indicates some difference in the rate of fall. The largest percentages of spores of *P. triticea* (table 4) were deposited on the slides during the 90-120 and 120-150 second periods. In the case of *P. graminis* the heaviest deposits occurred during the 120-150 and 150-180 second periods, while for *P. coronata* the heavy spore deposits were made in the periods from 150 to 180 seconds and from 180 to 210 seconds. A larger percentage of spores of *P. triticea*, there-

fore, fall more rapidly than those of other rusts. Two and one-half minutes after liberation, 71.6 per cent of the spores of this rust had fallen the length of the cylinder, 52.9 per cent of the spores of *P. graminis tritici*, 43.2 per cent of those of *P. graminis secalis*, and only 25.0 per cent of *P. coronata* spores.

The greatest variation in rate of fall was found in spores of *P. graminis secalis*. It is quite probable, however, that the four spores of this rust caught during the first minute after liberation fell part of the distance in a cluster, thus explaining how they could traverse the distance in so short a time. However, the cohesiveness of urediniospores appears to be great, and it is doubtful if, in many cases, single spores were separated from groups during their drop in the cylinder.

The average number of seconds required for the single spores of the four different rusts to fall 180 cm. and the average rate of fall are shown in table 5. The means were calculated from the formula $\sum fx/N$ when f = the frequency in a class (number of spores deposited on each slide during each 30-second period in this case), x = the class center, and N = the total number of spores.

TABLE 5
Average rate of fall in still air of urediniospores of four cereal rusts

CEREAL RUSTS	AVERAGE NO. SECONDS REQUIRED TO FALL 180 CM.	AVERAGE RATE OF FALL (MM. PER SECOND)	CALCULATED TIME REQUIRED TO FALL 1,000 FT
<i>Puccinia graminis tritici</i>	155.63 ± 0.41	11.57 ± 0.03	7 hrs., 19 min.
<i>P. graminis secalis</i>	170.09 ± 0.76	10.58 ± 0.05	8 hrs.
<i>P. coronata</i>	180.13 ± 0.50	10.00 ± 0.03	8 hrs., 28 min.
<i>P. triticea</i>	142.60 ± 0.83	12.62 ± 0.07	6 hrs., 43 min.

As each slide was exposed for 30 seconds, it was necessary in calculating the means and probable errors to use a class center. The mean of each exposure period was used; for example, all spores deposited on the slide exposed during the period from 60 to 90 seconds after liberation were considered to have fallen 180 cm. in 75 seconds, while for those caught during the period 90–120 seconds, 105 seconds was taken as the class average. With this method the assumption is made that the spores were deposited on the slides uniformly throughout each exposure period, although this probably did not occur. The slight error thus introduced would have very little effect on the means, as the variations would be in both directions. The probable errors of the means were calculated from the formula

$$P. E. = .6745 \sqrt{\frac{\sum fx^2}{N} - \bar{x}^2} \quad \text{where } x = \text{the class center, } f \text{ the class frequency,}$$

$$\sqrt{N}$$

\bar{x}^2 = the mean, and N = the total number of spores. From table 5 it is seen that the urediniospores of *P. triticina* fall more rapidly than those of the other three rusts, while *P. coronata* has the slowest average rate of fall.

The average velocity of fall of urediniospores of *P. graminis tritici* was found to be approximately 11.5 mm. per second, or a millimeter per second less than that of *P. triticina*, and 1 mm. more than the spores of *P. graminis secalis*. But the variation among spores of the same rusts was much greater than the variation between spores of the different rusts. In comparing the difference between the means (table 6), it is found that they exceed their

TABLE 6

Summary of differences between the means of the rate of fall of urediniospores of four cereal rusts in still air in a closed cylinder

RUSTS COMPARED	DIFFERENCE IN MEANS (MM. PER SECOND)	DIFFERENCE DIVIDED BY P.E.
<i>Puccinia graminis tritici</i> and <i>P. triticina</i>	1.05 \pm 0.076	13.82
<i>P. graminis tritici</i> and <i>P. graminis secalis</i>	0.99 \pm 0.053	17.07
<i>P. graminis tritici</i> and <i>P. coronata</i>	1.57 \pm 0.042	37.33
<i>P. triticina</i> and <i>P. graminis secalis</i>	2.04 \pm 0.06	23.72
<i>P. triticina</i> and <i>P. coronata</i>	2.62 \pm 0.076	34.47
<i>P. graminis secalis</i> and <i>P. coronata</i>	0.58 \pm 0.058	10.00

probable errors 10 times or more and are therefore undoubtedly statistically significant. The chances are infinitesimally small that these differences are due to errors of random sampling. It may be concluded, therefore, that there is a significant difference in the rate of fall of urediniospores of the four rusts studied under the conditions of the experiment. The urediniospores of *P. triticina* fall most rapidly, those of *P. graminis tritici* somewhat more slowly than those of *P. triticina*, but more rapidly than those of *P. graminis secalis* and *P. coronata*, while spores of *P. graminis secalis* fall slightly more rapidly than those of *P. coronata*, which have the slowest rate of fall.

Special mention may be made of the difference between the rate of fall of spores of *P. graminis tritici* and that of spores of *P. graminis secalis*, physiologic varieties of the same species of rust. The difference of 0.99 mm. per second is 17.07 times its probable error and therefore can not be attributed to random sampling. Levine (1923) found a significant difference in size of urediniospores of these two rusts when grown under uniform conditions. The spores of *P. graminis tritici* averaged 5.26 μ longer and 2.60 μ wider than those of *P. graminis secalis*. This might easily account for the difference in rate of fall, as the velocity of fall of the larger spores would be greater, assuming the density to be the same.

The foregoing results are interesting when considered from the standpoint of wind dissemination of urediniospores. Table 5 gives the time required for the average spore of the various rusts studied to fall 1,000 ft. in still air, based upon their rate of fall as determined under the conditions of the experiment. In the case of *P. graminis tritici*, over seven hours would be required for urediniospores to reach the ground from this elevation, provided no air currents influenced the fall. As spores are known to be numerous at much higher elevations, it is apparent that urediniospores of rusts as well as spores of other fungi can be carried long distances by strong winds, unless precipitated by rain or dew or influenced by convection currents.

RATE OF FALL OF AECIOSPORES

The common barberry has long been known to be a source of inoculum of black stem rust of grain and grasses. Many observations have been made on the development of local epidemics of stem rust near barberry bushes. Christensen² described the development of a local epidemic in 1922 near Northfield, Minn., where primary infection was traced for a distance of two miles from a group of infected barberry bushes.

No direct evidence of long-distance dissemination of aeciospores has been presented, but it seems probable that they may be carried considerable distances by air currents. Stakman et al. (1923) caught aeciospores on vaseline-covered slides exposed over infected barberry bushes at altitudes ranging from 100 to 7,000 ft. This indicates that aeciospores are carried upward to high altitudes, as well as urediniospores. It appears, therefore, that under favorable meteorological conditions they could be transported long distances and thereby serve as inoculum for areas at considerable distances from the infected bushes.

The rate of fall of aeciospores may be important when considering their long-distance dissemination by winds. Accordingly, the rate of fall of aeciospores of *Puccinia graminis tritici* and *P. graminis secalis* was determined by the method already described. The time required for 700 spores of each variety of rust to fall 30 cm. was recorded.

That some aeciospores were being liberated in clusters of several spores was soon evident after watching the fall of the spores in the glass cylinder. Particles of larger size and falling at a more rapid rate than the majority were observed. Especially was this true at the beginning of the discharge of spores from a particular spore horn. Often pieces of the spore horn would break off and fall to the bottom of the cylinder. In order to determine what these more rapidly falling particles were, the bottom of the cylinder was

² From unpublished observations made by Dr. J. J. Christensen.

removed and some of them caught on vaseline-covered glass slides. Examination of these slides under the microscope showed that some of the aeciospores were in short chains and clusters of varying numbers. By far the greatest number of particles, however, were single aeciospores.

Particles of apparently larger size and falling faster than the majority were disregarded and the rate of fall of only what appeared to be single spores recorded. This was not difficult, however, as often hundreds of spores falling more or less uniformly could be seen in the cylinder at one time. That a variation existed in the rate of fall of single spores was evident after watching the process for a time. Spores that appeared to fall approximately at the same rate would gradually become separated because of a difference in their rate of fall. On the other hand, it was observed that

TABLE 7

Number of aeciospores of two varieties of Puccinia graminis that fell 30 centimeters, in a glass cylinder, in different lengths of time, and their average velocity

TIME (IN SECONDS)	NUMBER OF SPORES	
	TRITICI	SECALIS
20	2	—
21	4	—
22	10	5
23	19	31
24	40	37
25	62	50
26	95	57
27	83	64
28	73	81
29	62	87
30	60	80
31	49	48
32	45	34
33	39	22
34	20	15
35	20	14
36	12	13
37	5	13
38	—	11
39	—	10
40	—	9
41	—	7
42	—	6
43	—	4
44	—	2
Average time	28.4 ± 0.09	29.4 ± 0.11
Average velocity (in mm. per second)	10.56 ± 0.03	10.20 ± 0.04

several spores would sometimes maintain their same positions relative to each other all the way down the cylinder.

All the data on rate of fall were obtained in a basement room in which the temperature was relatively constant. Convection currents within the cylinder could, of course, influence the rate of fall of the spores, but in practically all cases the spores fell in a direct line without noticeably changing their rate or direction of fall. Care was always exercised not to touch the cylinder during the trials. If, as in a few cases, convection currents

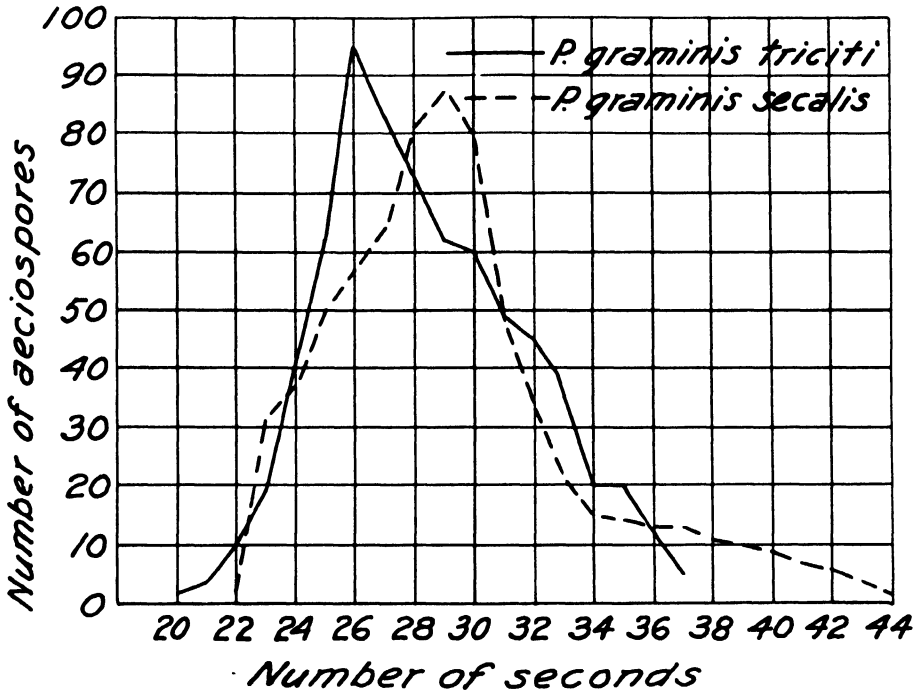


Fig. 3.—Variation in the time required for aeciospores of two varieties of *Puccinia graminis* to fall 30 centimeters in a glass cylinder.

seemed to be influencing the path of the spores, no measurements were recorded.

The action of convection currents could easily be demonstrated by placing the hand at the bottom of the cylinder. When this was done, the body heat soon set up convection currents inside the cylinder, which would not only influence the rate of fall of spores but would actually carry spores upward from the bottom to the top of the cylinder. Because of the fact that these induced convection currents could easily be observed, it is thought that if currents strong enough to influence the rate of fall had been present when measurements were made, they also would have been observed.

There was considerable variation in the rate of fall of aeciospores under the conditions of the experiment, as shown in table 7 and graphically in figure 2. The range in the time required to fall 30 cm. was from 20 to 37 seconds in the case of *P. graminis tritici* and from 22 to 44 seconds for *P. graminis secalis*. Aeciospores of *P. graminis tritici* fell at an average rate of 10.56 ± 0.03 mm. per second, and those of *P. graminis secalis* at 10.20 ± 0.04 mm., the difference being 0.36 ± 0.05 mm. per second. This difference

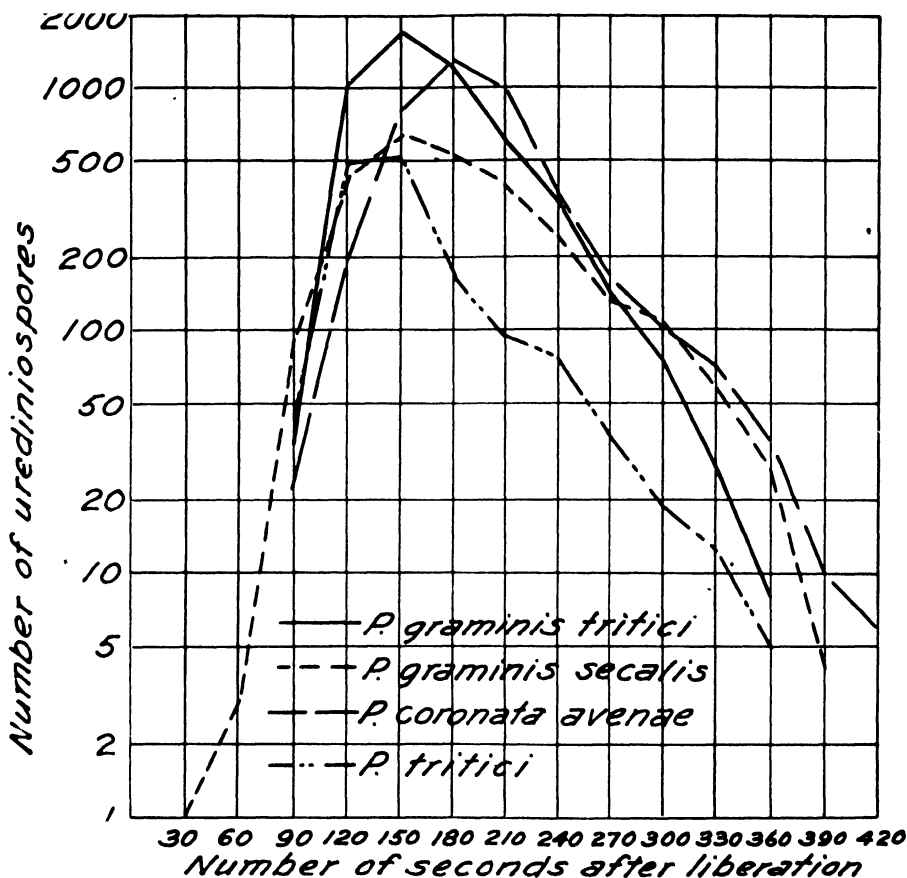


Fig. 4.

is more than seven times its probable error and therefore statistically significant, the chances being more than 400,000 to 1 that it was not due to random sampling. This difference in rate of fall may be due to difference in spore size, as in the case of urediniospores. Levine (3) found that aeciospores of *P. graminis tritici* averaged 2.62μ longer and 2.20μ wider than those of *P. graminis secalis*.

It is interesting to note that urediniospores of *P. graminis tritici* also

have a higher rate of fall and are somewhat larger than urediniospores of *P. graminis secalis*. When comparing the rate of fall of urediniospores and aeciospores, it is found that urediniospores of *P. graminis tritici* fall approximately 1 mm. per second faster than aeciospores, while the urediniospores of *P. graminis secalis* fall 0.38 mm. per second faster than the aeciospores. In both cases the urediniospores are larger than aeciospores.

The size of spores can not be considered the only factor responsible for the differences in the rate of fall. Density and shape might also be important, but the size of spores would influence the rate of fall if the other two variables were constant.

As aeciospores fall more slowly than urediniospores in still air, their dispersal distance would theoretically be greater than that of urediniospores under similar meteorological conditions. The rate of fall of aeciospores indicates that they could easily be carried to high altitudes by convection currents, as well as long distances by favorable winds.

In order to test the accuracy of the two methods used in measuring the rate of fall of spores, the rate of fall of urediniospores of *P. graminis tritici* was measured by the method used in determining that of aeciospores.

A leaf of Little Club wheat, heavily infected with the uredinial stage of

TABLE 8

Number of urediniospores of Puccinia graminis tritici that fell 30 centimeters, in a glass cylinder, in different lengths of time, and their average velocity

TIME (IN SECONDR)	NUMBER OF SPORES
18	3
19	5
20	11
21	23
22	31
23	44
24	57
25	57
26	63
27	48
28	38
29	36
30	26
31	20
32	13
33	13
34	9
35	3
Average time	20.07 ± 0.11
Average velocity (in mm. per second)	11.51 ± 0.05

P. graminis tritici, was fastened to the glass rod used to hold the infected barberry leaves. By gently tapping this rod, urediniospores were induced to fall to the bottom of the cylinder. It was then possible to measure their rate of fall by the method used for aeciospores. The time required for 500 urediniospores to fall 30 cm. was determined in this manner. Results are given in table 8. It will be seen that the average rate of fall for 500 urediniospores was 11.51 ± 0.05 mm. per second as determined by this method. The rate of fall for urediniospores of *P. graminis tritici*, determined by using the galvanized cylinder, was 11.57 ± 0.03 , the difference between the two methods being 0.06 ± 0.06 mm. per second. This difference is only as great as its probable error and, therefore, probably due to chance.

The two methods used were quite different but gave practically the same results. This would indicate that both methods were accurate.

DISCUSSION AND CONCLUSIONS

The theoretical dispersal distance of a rust spore would be determined by its rate of fall, altitude attained, and wind velocity. Assuming that an average urediniospore of *P. graminis tritici* had reached an altitude of 5,000 ft., it would require 36 hours and 35 minutes to reach the ground. If it were being carried by a 30-mile wind its dispersal distance would be approximately 1100 miles. With the great variation that exists in rate of fall of spores of any one rust, the theoretical dispersal distance would also vary. About 45 per cent of the urediniospores of *P. graminis tritici* fall more slowly than the average, and their dispersal distance would accordingly be increased. Although differences exist in the average rates of fall of urediniospores of the four rusts studied, they are of minor importance when considered from the standpoint of long-distance dissemination. The spores of all rusts fall so slowly that after having reached a high altitude they would be carried long distances under favorable conditions. In the hypothetical case outlined above, urediniospores of *P. graminis tritici* were shown to have a dispersal distance of approximately 1100 miles. Under the same conditions, *P. triticea* would have a theoretical dispersal distance of approximately 1,000 miles, *P. graminis secalis* 1,200 miles, and *P. coronata* 1,270 miles. With the variation that exists within each rust, a few spores of each would be carried approximately the same distance. The greatest difference would be in the percentage of spores of each rust carried different distances. A larger percentage of urediniospores of *P. coronata avenae* would be carried a given distance than spores of the other rusts studied.

In nature, air currents no doubt are important factors in the time required for a spore to reach the ground from a given altitude. The fact that

spores reach elevations of 10,000 ft. indicate that they are rather easily carried upward against the force of gravity. With the currents and cross currents that exist in nature, the paths of spores being carried long distances can only be conjectured. A spore transported at the rate of one mile an hour would travel at the speed of 447 mm. per second. This is 39 times as fast as the average spore of *P. graminis tritici* falls in still air. According to the *Official Record*³ for November 20, 1930, a wind blowing at less than one mile an hour allows smoke to rise vertically and therefore would not be perceptible. A convection current traveling upward from the ground at the rate of 1/38 mile an hour or more would carry spores upward as long as these currents continued. Currents at that speed would not allow spores to drop. Convection currents no doubt travel downward as well as away from the earth's surface at various times and would carry with them spores from the upper air. The combined effect of gravity and convection currents would greatly increase the rate of fall of spores; therefore under certain atmospheric conditions the dispersal distance would be greatly reduced.

That urediniospores of stem rust which develop early in Mexico and Texas could be transported in a few days to the spring wheat area of the United States is at least theoretically possible. It also seems reasonable to suppose that sometime during the growing season conditions are favorable for such transportation to take place. The rate of fall of aeciospores also indicates that they too may be carried long distances and that therefore the common barberry may serve as a source of stem-rust inoculum for fields at considerable distances from infected bushes.

SUMMARY

1. Clusters of urediniospores fall at a higher average rate of speed in still air than single urediniospores.
2. The average rate of fall of clusters of spores increases as the number of spores in a cluster increases.
3. The average rate of fall in still air of urediniospores of *Puccinia graminis tritici* was found to be 11.57 ± 0.03 mm. per second, for *P. graminis secalis* 10.58 ± 0.05 , for *P. coronata avenae* 10.00 ± 0.03 , and for *P. triticina* 12.62 ± 0.07 mm. per second.
4. The observed difference in the rate of fall of urediniospores of the four cereal rusts was found to be statistically significant.
5. The velocity of fall of aeciospores of *P. graminis tritici* and *P. graminis secalis* was found to be less than that of urediniospores of these rusts.

³ The Official Record. U. S. Department of Agriculture.

6. The rate of fall of aeciospores of *P. graminis tritici* and *P. graminis secalis* in still air was 10.56 ± 0.03 and 10.20 ± 0.04 mm. per second respectively.

7. The observed difference in rate of fall of aeciospores of the two varieties of rust was found to be statistically significant.

8. The average theoretical dispersal distance of urediniospores that have reached an altitude of 5,000 feet and are being carried by a 30-mile wind ranged from 1,000 miles for *P. triticina* to 1,270 miles for *P. coronata*. Under the same conditions *P. graminis tritici* would have an average dispersal distance of 1,100 miles and *P. graminis secalis* 1,200 miles.

9. The average theoretical dispersal distance of aeciospores, based on their rate of fall, is greater than that of urediniospores.

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INDEX TO AMERICAN BOTANICAL LITERATURE 1930-1932

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The life history and cytology of *Protosiphon botryoides*

HAROLD C. BOLD

(WITH PLATES 10-19 AND SEVEN TEXT FIGURES)

INTRODUCTION

From the numerous studies of nuclear and cell division in many types of organisms of both the plant and animal kingdoms there have emerged the striking facts of the essential similarity of karyokinesis throughout a wide range of organisms, and secondly of the apparent existence of several distinct categories of cytokinesis. In the plant kingdom especially the occurrence of varied methods of cell division has been repeatedly demonstrated. Furthermore nuclear and cell division may be closely related through the medium of the kinoplasmic achromatic figure as in the higher plants, or totally unrelated processes as in certain fungi. Reported observations of nuclear and cell division in fungi are numerous, but there have been few modern accounts dealing with the same processes in the algae and it is still a question whether the type of cytokinesis (progressive cleavage) characteristic of the coenocytic sporangia of the fungi, has a counterpart in the swarmspore and gamete formation in algal zoosporangia. McAllister's recent (1931) report of cell division by phragmoplast and cell plate in *Spirogyra setiformis* suggests that similar studies of other algae may be fruitful in clarifying the categories of cell division.

Among the various forms of Chlorophyceae whose life histories and cytological characters are still somewhat obscure are *Botrydium* Wallroth of the Heterokontae and *Protosiphon* Klebs, which up to the studies of Klebs (1896) were considered to be identical. The life history, habit of growth and cell structure of *Protosiphon* present many features which suggest simultaneously the characters of the more primitive Chlorococcales such as *Chlorococcum* and the more highly developed Siphonales. *Protosiphon* is included in the Chlorococcales by such authorities as West and Fritsch (1927), Printz (1927), Brunnthaler (1915) and Oltmanns (1922). On the other hand, Setchell and Gardner (1920) and West (1916) include the family Protosiphonaceae among the Siphonales.

The present study of these genera was undertaken primarily with the view of giving a more complete account of their life history, cell structure and cytology. The following paper deals exclusively with *Protosiphon botryoides* Klebs. This investigation was carried on in the Botanical Labo-

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ratory of Columbia University with the aid of a University Fellowship, and I take this opportunity of acknowledging my appreciation of the fellowship and of expressing my gratitude to Professors R. A. Harper and J. S. Karling for stimulating criticisms and suggestions. I should also like to thank Professors T. E. Hazen and C. C. Curtis for suggestions and valuable discussion during the progress of the work.

SUMMARY OF THE LITERATURE

The general features of the structure and reproduction of *Protosiphon botryoides* have become fairly well known through the studies of Cienkowski (1855), Rostafinski and Woronin (1877), and especially Klebs (1896). Briefly summarizing the results of these investigators, one concludes that development and reproduction of this organism may occur in several ways. First, under conditions of drought the thallus protoplast may break up into a number of more or less spherical segments or "spores" which are enclosed by walls, develop a red pigment and enter upon a resting period. Depending on subsequent conditions of their environment these "spores" may produce zoospores or grow directly into thalli. Secondly, the thalli produce zoospores when submerged in water. The zoospores may develop without fusion directly into new plants, or, conjugating in pairs, form star-shaped zygosporangia which after a period of dormancy germinate into new thalli. Klebs has reported the division of young cells and thalli by bipartition. Strasburger (1897) confirms Klebs' observations on the life history of *Protosiphon*. With the exception of Miss Carter's note (1926) that this alga is monoecious, there have been no other contributions to our knowledge of *Protosiphon*.

In my study of this organism I have given particular attention to the method of cytokinesis and shall include the summary of the data on this subject at this point.

Since the time of Timberlake's description of zoosporogenesis in *Hydrodictyon* there has been comparatively little detailed cytological study of the process of cytokinesis in the Chlorophyceae in general. This paucity of data is quite significant and striking in view of the fact that these algae are to many polyphyletists the probable ancestors of many of the lower fungi and Phycomycetes, in which cytokinesis is fairly well known. In phylogenetic studies of the Chytridiales, Zygomycetes and Oomycetes considerable emphasis has been placed on characters such as the capacity to form motile reproductive cells at some time during the life cycle, as being in some manner indicative of phylogenetic relationship; but comparatively little significance has been attached to the similarity or difference in the process by which such motile cells are formed. As early as

1902 Timberlake suggested that such comparative studies of spore formation might be fruitful, but apparently few investigators have up to the present time interested themselves in this problem.

The literature of spore formation in the Thallophyta is too extensive to permit of complete review at this time. Harper (1899, 1900, 1914), Timberlake (1902) and Schwarze (1922) have adequately summarized the earlier data with especial reference to the fungi, and I shall accordingly limit my résumé to cytokinesis in the Chlorophyceae and those fungi whose spore formation is analogous to the process in *Protosiphon*.

The conception of free cell-formation which for so many decades influenced students of cell multiplication has played an important part in the observation and description of spore formation in the Thallophyta. It has been carried over in more modern times in the accounts of simultaneous cleavage by such investigators as Kusano (1909), Curtis (1921), Bristol (1920) and others. Harper (1899) and Schwarze (1922) have pointed out that the difficulties of studying thick, opaque sporangia in the living condition and at high magnification undoubtedly explain the discrepancies between the earlier accounts of spore formation and those based on more modern methods of fixation, sectioning and staining. Harper demonstrated by means of this technique that a great many stages of cleavage had been overlooked. According to his account, in *Synchytrium decipiens*, *S. Taraxaci*, *Pilobolus crystallinus* and *Sporodinia grandis*, spore formation does not consist of a simultaneous fragmentation whereby the protoplasm of the sporangium is at once cut up into a number of polyhedral segments, as Dangeard (1890) had described it in *Synchytrium*; it is rather a progressive process occupying various periods of time from about one hour in *Sporodinia* to six in *Pilobolus*. The process is markedly progressive, since furrows originate at different regions of the surface (not always simultaneously) and cut progressively deeper into the protoplasm, thus delimiting at first large segments with many nuclei, which are subsequently divided by secondary furrows into smaller, either multinucleate spores (*Sporodinia*) or uninucleate spores (protospores) (*Synchytrium decipiens*). The furrows may be quite sharp and deep as they cut through the spore plasm, or quite broad; from Rothert's (1892), Davis' (1903) and Schwarze's (1922) accounts of oogenesis and swarmspore formation in the Saprolegniales it seems to be true that the depth and width of the furrows are correlated with the volume of protoplasm within the sporangium and oogonium; broad and shallow furrows are characteristically formed when the primordial utricle is thin, while sharp and deep furrows arise when the dense protoplasm fills the cell cavity. The various genera studied show some interesting modifications of this process which are significant in the

light of the process in algal forms. In *Synchytrium decipiens* the uninucleate segments are not the definitive spores, but become multinucleate, increase tremendously in size and at germination produce the swarmspores. This period of nuclear division and cell enlargement following cleavage Harper called an embryonic stage; and the primary uninucleate segments he termed protospores. In *S. Taraxaci* the process is simplified by the omission of the protospore stage, the multinucleate segments delimited by the primary cleavage furrows functioning directly as spores which germinate as zoosporangia. In *Pilobolus* the protospores undergo a period of nuclear and cell division by constriction following which bi-nucleate spores are finally formed. In *Sporodinia* the primary cleavage furrows delimit multinucleate masses of spore plasm which round off and function as the definitive spores. The process here is essentially the same as in the other genera, but more rapid and abbreviated and produces thinner-walled spores. Harper suggested that the difference in time and conditions of germination between the spores of *Sporodinia* and *Pilobolus* may be correlated with the difference in the rates of the cleavage processes by which they are formed.

Not all investigators are in agreement as to the method of spore formation in *Synchytrium*. Kusano (1909) reports that *S. Puerariae* "does not form protospores, as is the case in *S. decipiens* (Harper, 1899, p. 488)" and has two different methods of division. The first is very similar to that described by Harper for *S. decipiens*, spore formation being accomplished by surface furrows, which cut progressively deeper into the protoplasm and with the aid of secondary furrows eventually cut out multinucleate segments. Kusano agrees with Harper that cleavage is accompanied by loss of water and extrusion of oil droplets. In addition he reports a second type of cleavage which is not accompanied by loss of water but consists of a simultaneous precipitation of membranes between the nuclei throughout the thallus, resulting in the formation of equal-sized, polyhedral segments. In view of Harper's observation that when the protospores of *S. decipiens* are completely delimited they undergo a period of rapid swelling, completely fill the sporangial cavity, and assume a polyhedral shape so that they appear to be separated by fine granular plates, one is inclined to question Kusano's description. The stage of simultaneous precipitation of membranes between the nuclei in spore formation may well be that of the swollen and closely appressed, yet completely delimited segments (embryonically germinating protospores) described by Harper. Kusano points out a supposed analogy between his process of internuclear membrane formation and Timberlake's (1902) description of zoosporogenesis in *Hydrodictyon*: "The compact cytoplasmic mass produces partitions between two adjacent nuclei, as Timberlake (1901) observed in the formation

of the swarmspores in *Hydrodictyon*." That there is no similarity between Kusano's simultaneous cleavage in *Synchytrium* and the process in *Hydrodictyon* becomes at once apparent on recalling Timberlake's description in which he states: "Cleavage itself is, as Klebs pointed out, a progressive process; . . . In the first stages in the process short furrows that have no apparent orientation with reference to one another or to the nuclei appear here and there through the cytoplasm (Fig. 22). Seen in a surface section these furrows appear as single lines and thus might easily be taken for cell plates formed in the protoplasm without the help of visible spindle fibers; but if a vertical section is studied the appearance of furrows becomes manifest (Figs. 31, 32)". "We have such coenocytic cells as the fungus sporanges and the *Hydrodictyon* cell where there is a progressive cleavage by means of surface constrictions." There exists no similarity between Kusano's simultaneous cleavage by membranes in *Synchytrium Puerariae* and the progressive cleavage in *Hydrodictyon* if we accept Timberlake's account. Neither Harper (1899) nor Kusano describes the segmentation of the spores as sporangia with the formation of swarmspores. In a more recent report on the life history and cytology of *S. fulgens*, Kusano (1930) describes formation of the spores from the thallus as a process of simultaneous cleavage by formation of "plasmic walls" between the nuclei, which is apparently similar to the process he reports in *S. Puerariae*. Another recent investigator, Curtis (1921), reports that there are about thirty-two nuclei in the thallus of *Synchytrium endobioticum* at the time of cleavage and that "the walls appear simultaneously throughout the organism" forming the spores. The spores germinate as sporangia and become highly vacuolate by absorbing water prior to zoospore formation. Miss Curtis describes the delimitation of the zoospores as follows: "Separating the vacuolated areas, and intersecting one another roughly at right angles, are short strands of protoplasm which have retained their original density, and by the combined intersections of which the delimitation of the zoospore areas is effected (fig. 63)." In the light of Swingle's (1903) observations of cleavage in *Phycomyces* sporangia, it would seem possible that the process of zoospore formation in *Synchytrium endobioticum* also can be interpreted as being accomplished through the active agency of vacuoles, rather than through the agency of the intersecting protoplasmic strands, as Miss Curtis regards it.

Kusano (1921) further finds no evidence of progressive cleavage in *Olpidium Viciae* but reports "that a clear space appeared in the cytoplasm, all at once between each two nuclei, and that the protoplasm was cut up into as many polygonal segments as there were nuclei." Wager (1913) reports that cleavage in *Polyphagus Euglenae* begins at the center

and proceeds toward the surface of the sporangium, a process very similar to that described in oogenesis and sporogenesis in *Saprolegnia*.

With the possible exception of the Saprolegniales, the Zygomycetes have been the objects of most intensive investigation as to their method of spore formation. Harper (1899), Swingle (1903) and Schwarze (1922) have studied a series of representative forms including *Pilobolus*, *Sporodinia*, *Rhizopus*, *Phycomyces*, *Mucor* and *Circinella*. These investigators agree that spore formation is accomplished by progressive cleavage by surface furrows which cut in from the periphery of the sporangium and in some cases also from the columella region. In *Phycomyces* the spores are delimited by vacuoles which gradually become angular and fuse. These authors agree that the columella is formed from a dome shaped layer of vacuoles, which become angular and fuse at their edges, thereby separating the spore plasm from the columella plasm, and in this cleft the columella wall is subsequently deposited. In *Pilobolus* in addition to the dome-shaped layer of vacuoles, cleavage furrows cutting up from the base of the sporangium are active in columella formation.

The Saprolegniales show a similar process of cleavage in the formation of zoospores. Rothert (1892), Davis (1903) and Schwarze (1922) describe the formation of cleavage furrows from the surface of the central vacuole which cut centrifugally through the protoplasm, isolating the zoospore initials. As the cleavage furrows cut through the plasma membrane contraction occurs due to the escape of cell sap through the sporangium wall. The delimited spore initials round up and then expand, forming closely appressed polygonal masses, between which the cleavage furrows appear as delicate lines. Then follows a second contraction stage during which the spores separate, round up and become mature. Schwarze points out that the rapidity with which the spore initials are delimited, contract, and expand, and the fact that there are two contraction stages have led to the false conclusion that spore formation is simultaneous. In addition to sporangia in which the protoplasm occurs as a peripheral layer surrounding a large central vacuole, there are others densely filled throughout. In the first type Rothert describes the heaping up of the protoplasm at definite regions along the plasma membrane which thus become separated by broad furrow-like areas. According to Schwarze the furrows deepen progressively in cutting through the spore plasm, but Rothert maintained that they appeared simultaneously in their entire depth. Cleavage in densely filled sporangia without a central vacuole is effected through the formation of a central, longitudinal cleft, from which smaller furrows cut through the spore plasm in centrifugal fashion toward the surface.

In the Myxomycetes as well, the evidence in the literature points

strongly to spore formation by progressive cleavage. In *Ceratiomyxa* of the Exosporeae Olive (1907) found that the fruiting stalks were composed of a central layer of gelatinous material on whose surface is spread a very thin layer of multinucleate spore-plasm which is later divided by broad furrows into uninucleate segments. Olive notes that the surface spore-plasm of one region of the stalk may have reached the condition of uninucleate segments while in other regions cleavage is just beginning. No nuclear divisions occur immediately before or during cleavage. The uninucleate segments or protospores round off and become the definitive spores, borne on sterigmata. Olive describes the spore nuclei as passing through a period of synapsis followed by two rapid nuclear divisions so that the mature spores are tetranucleate. He regards these two nuclear divisions as reduction divisions. In general they would correspond to the embryonic stage which Harper described.

Of the Endosporeae Harper (1900, 1914) has studied *Fuligo* and *Didymium*. In *Fuligo* the nuclei are more or less aggregated into groups before cleavage begins. Furrows form at the surface of the aethalium and cut in at all angles. They may be narrow with sharp edges, or broad, curved and forked. The primary cleavage furrows do not cut through the entire mass of spore-plasm but curve and fork so as to delimit superficial segments. New furrows not continuous with the first appear and cut up the central protoplasm into multinucleate blocks. Meanwhile the surface segments are further subdivided into fragments with one or several nuclei. The central portion of the aethalium, however, may be still multinucleate and undivided by the time the surface segments have reached the uninucleate stage. At the time the superficial segments are forming, nuclear divisions begin and continue during the entire process without any apparent direct relation to it. The ultimate cleavage segments function as spores without further divisions and growth such as occur in *Synchytrium decipiens*.

Cleavage in *Didymium* is essentially similar to that described for *Fuligo*. Radial furrows appear along the capillitial threads near the columella and on the outer surface of the sporangium. Later tangential furrows originate at the primary furrows, and move into the protoplasm, delimiting small multinucleate masses. These are further subdivided until the uninucleate segments are formed. These function directly as the definitive spores as in *Fuligo*. Probably only a single division of the nuclei takes place while cleavage transpires. Bisby (1914) described a similar method of cleavage in the sporangia of *Physarella mirabilis* and *Stemonitis fusca*. Vonwiller (1919) figures spore formation in *Lycogala* as a process of progressive cleavage proceeding from the center toward the periphery of the maturing fruiting body. More recently Howard (1931) in a detailed account of the

life history of *Physarum polycephalum* describes and figures spore formation as progressive cleavage by furrowing, very similar to that which Harper had described in *Fuligo*.

It would appear from the above mentioned cases that the bulk of the evidence indicates that spore formation in the coenocytic sporangia of Chytrids, Zygomycetes, Oomycetes and Myxomycetes is by progressive cleavage.

As to the method of cytokinesis in the Chlorophyceae fewer data are available. This is doubtless to be accounted for in part by the presence of chlorophyll, starch grains, and oil droplets, which makes the study of spore formation more difficult than in the fungi. Many of the earlier students of the algae regarded spore formation as a simultaneous division of the protoplasm in the zoosporangium. Such an account is given by Famintzin (1871) for *Chlorococcum infusionum*. Cohn's (1875) description of spore formation in his newly described *Chlorochytrium Lemnae* suggests that the process is somewhat similar to that in *Synchytrium decipiens*, and in certain respects to that in the densely filled sporangia of *Saprolegnia*. Cohn describes this process as follows: "Endlich tritt in dem grünen Protoplasma eine eigenthümliche Art der freien Zellbildung auf, indem sich an verschiedenen Punkten der Zellhöhle in der Nähe der Wand Ansammlungen des grünen Inhalts bilden, die nach innen vorspringende Wellenberge darstellen, und durch Wellenthälern von geringerer Tiefe unter einander getrennt sind (Fig. 5g). Indem das in den Wellenthälern enthaltene grüne Plasma allmählich ganz und gar nach den Wellenbergen wandert werden diese von einander völlig isolirt; so zerfällt das grüne Plasma der Endophytenzelle in eine grosse Zahl von Segmenten, die, gleich Dotterkugeln eines gefurchten Froschei, dicht an einander gelagert sind (Fig. 5, e, f.). . . . Schliesslich zerfallen die segmente wieder in einer Weise, die ich wegen ihrer Undurchsichtigkeit nicht specieller zu verfolgen vermochte (Fig. 5 g. h.), in einer ausserordentlich grosse Zahl birnformiger Zoosporen, welche dicht aneinandergedrängt, die Höhle ihrer Mutterzelle ausfüllen (Fig. 5 g. h.)." The similarity between the polygonal segments which Cohn describes and figures and the uninucleate protospores of *Synchytrium decipiens* is very striking, and the further development of these segments into swarmspores in *Chlorochytrium* seems comparable to the embryonic stage in *Synchytrium*. Klebs (1881) describes zoosporogenesis in *C. Lemnae* as a process of successive bi-partition. Miss Bristol (1920) does not comment on sporogenesis in *C. Lemnae* Cohn, but reports in *C. bienne* that the process is one of bi-partition. Furthermore, in *C. paradoxum* she reports that the protoplast contracts into an irregular globose mass, and the space between its boundary and the cell wall becomes filled with

reddish or orange colored granules. This mass divides into two parts, each of which by further bipartition forms zoospores. The author adds: "During this process of division a rejuvenation of the protoplasm takes place, so that the completed zoospores entirely fill the cell cavity." Miss Bristol does not figure this process of bipartition, but several points in her discussion indicate strongly that the process may be progressive cleavage. The loss of water and contraction of the protoplast before or during the spore-forming divisions, the elimination of waste and granular material from the protoplast, and the so called "rejuvenation"—swelling of the spore initials, are phenomena usually associated with the progressive cleavage of a coenocyte. Miss Bristol (1917) described a new species of *Chlorochytrium*, *C. grande*, which produces both zoospores and aplano-spores which are morphologically equivalent; however, she states that the former arise by bipartition of the protoplast and the latter by its simultaneous division.

In a more recent paper Geitler (1924) attempts to summarize the data on spore formation in the unicellular forms (Protococcales) in connection with his study of the development and structure of *Sorastrum spinulosum*. At maturity the cells of this organism are multinucleate and during zoospore formation the chromatophore divides by successive bipartition. According to him: "Die Fortpflanzung beginnt mit Teilungen des Chromatophors, der in mehrere Stücke, soviel als später Zoosporen entstehen, zerlegt wird. Meist teilt sich der Chromatophor zuerst in zwei Hälften, die dann Sukzessive in weitere Stücke zerlegt werden." The protoplast is divided by one or several clefts which may appear simultaneously; he states that part of the protoplasm does not enter into the zoospores but remains in the mother cell. He stresses the similarity between the process in *Sorastrum* and that in *Pediastrum*, *Tetraedron*, *Characium* and *Hydrodictyon* and concludes: "Dass Charakteristische für alle diese Formen ist, dass die Tochterzellen simultan, durch Zerklüftung des vielkernigen Plasmas entstehen, wobei das ungeteilte Pyrenoid aufgelöst und in den Tochterzellen neu gebildet wird." In view of Geitler's own description of zoospore formation in *Sorastrum*, Smith's (1916) and Harper's (1918b) accounts of *Pediastrum*, Smith's account of *Characium* (1916), *Tetraedron* (1918), *Scenedesmus* (1914) and Timberlake's account of *Hydrodictyon* (1902), it is difficult to understand why Geitler should state that these genera show simultaneous cleavage. On this same basis Geitler would divide the Proto-coccales into two groups. In the first class he would include forms such as "*Tetraedron*, *Characium*, *Scenedesmus*, *Coelastrum*, *Sorastrum*, *Pediastrum*, *Hydrodictyon*" which have "simultan" formation of the reproductive cells, while the second group would include genera like "*Chlorococcum*, *Chloro-*

chytrium, *Cystococcus*, *Chlorella*, *Dictyosphaerium*" in which the daughter cells are formed by successive bipartition. While one must commend Geitler's recognition of the fact that the finer details of cell structure and multiplication must be considered in phylogenetic systems, one can hardly agree with his present classification. His inclusion of *Chlorochytrium* and *Chlorococcum* in his second group is open to criticism. I have pointed out above the evidence that zoosporogenesis in *Chlorochytrium* is not by bipartition. There is some diversity of opinion as to zoospore formation in *Chlorococcum*. Famintzin (1871) reports that it is a simultaneous process in *C. infusionum*, while Artari (1892) describes it as bipartition in the same species. In my study of the same species (1931) I found that the swarmspores arose in the mother cell by a progressive cleavage of the protoplast in a manner very similar to that in *Sporodinia*. The aplanospores of *Chlorococcum* which are simply zoospores which, due to lack of moisture, are not liberated and omit the motile stage, are formed in an identical manner. In her account of *C. humicola* (1919) Bristol also emphasizes the complete homology between zoospore and aplanospore, and yet reports that they have a very different method of formation, the former by repeated bipartition and the latter by simultaneous fragmentation of the protoplasm of the parent cell. No explanation of this apparent contradiction is vouchsafed.

The remaining genera discussed by Geitler as far as I am aware have not been studied with particular attention to cell division. Among the Protococcales therefore two types of cell structure and division occur: the first category includes forms in which the cells are uninucleate and the daughter cells formed by bipartition, such as *Scenedesmus*, *Tetrademus*, and probably *Chlorella*; the second would include such genera as *Chlorococcum* (certainly *C. infusionum*), *Hydrodictyon*, *Characium* and probably *Sorastrum* and *Chlorochytrium*, forms in which the cells are coenocytic at least immediately preceding reproduction, and in which the reproductive cells are formed by progressive cleavage of the protoplast. I have omitted *Pediastrum* from both groups in view of the contradictory evidence available.

Of the Volvocales the conditions in *Chlorogonium*, *Gonium* and *Eudorina* may be considered typical of the group. Hartmann (1919) describes zoospore formation in the first genus as effected by a series of successive nuclear and protoplast bipartitions so that the number of spores produced is usually a multiple of two. A similar process with gelatinization of the mother cell wall is involved in the production of the daughter colonies in *Gonium* (Harper, 1912, Hartmann 1924) and in *Eudorina* (Hartmann, 1924).

Those members of the Ulotriconales which have been studied seem to indicate that the process here is similar to that in the Volvocales. Strasburger (1880), Gross (1931) and Cholnoky (1932) report that the zoospores and gametes of several *Ulothrix* species arise by consecutive nuclear divisions and bipartitions of the protoplast. Cholnoky (1928) describes a similar process in *Stigeoclonium tenue*.

There are several accounts of spore formation in *Cladophora*. Strasburger (1892) states that the zoospores in *C. laetevirens* and *C. lepidula* arise by clefts in the mother cell: "Zugleich wird der Wandbeleg durch rinnenformige, von innen nach aussen vordringende Vertiefungen in so viele Abschnitte zerlegt, als Zellkerne vorhanden sind." The primordial utricle is divided into polygonal masses by delicate plasma walls; according to Strasburger nuclear division precedes cleavage; the pyrenoids dissolve and arise *de novo* in the swarmspores, which contract toward the center of the cell when cleavage is completed as in *Hydrodictyon*; cilia develop from a kinoplasmic swelling of the plasma membrane. He describes an essentially similar process in *Bryopsis*, *Acetabularia*, *Siphonocladus*, and *Chaetomorpha*.

A more recent account based on fixed, sectioned and stained material is that of Miss Czerny (1930). In *Cladophora callicoma* and *C. glomerata* zoospore formation is initiated at the terminal cells of the branch and proceeds toward the basal; the nuclei multiply rapidly in preparation for swarmspore production; then the small chromatophore segments begin to collect around the nuclei as does the protoplasm, by a sort of 'heaping up' or flowing process. This description reminds one of Rothert's (1892) account of spore formation in those sporangia of *Saprolegnia* with central vacuoles. The threads of protoplasm still connecting the swarmspore initials are described as becoming finer until they ultimately disappear, leaving the spores completely delimited. There is some relation between this localized accumulation of protoplasm in *Cladophora* and Swingle's theory of localized contraction. In *C. glomerata* the chromatophore is more homogeneous. The protoplast contracts somewhat, the nuclei assume a peripheral position and the zoospore initials "kugeln sich entweder einzeln direkt vom übrigen noch ungeteilten Plasmamantel ab" etc. Although the author does not interpret the process in *C. glomerata* as one of progressive cleavage, her figures are very similar to Swingle's figures of *Rhizopus*, with the exception that uninucleate segments are formed immediately in *Cladophora*. Klebahn (1899) describes and figures oogenesis in *Sphaeroplea annulina* as effected by surface furrows which progressively cut through the protoplasm, delimiting the egg initials.

Davis (1908) reports the development of the large multiciliate zoospores

of *Derbesia* as a process of progressive cleavage by furrows which originate at the surface of the sporangium, delimiting first multinucleate and ultimately uninucleate segments. Miss Williams' (1925) account of the development of the gametangia in *Codium tomentosum* does not particularly discuss the method of formation of the male and female gametes from the multinucleate gametangia, but she suggests that the gametes are delimited simultaneously by walls.

MATERIAL AND METHODS

My original *Protosiphon* material was collected from clay soil from several different localities in the vicinity of New York City and was found intermingled with *Botrydium* on the same substratum. The soil which adhered to the plants made fixation and sectioning difficult and stimulated an effort to obtain pure cultures on artificial media. This was accomplished in the following manner. As the soil cultures of the plants slowly dried in bright sunlight the protoplasm of the thalli broke up into a number of rounded cells which Cienkowski (1855) first called 'spores.' With the help of a binocular dissecting microscope and finely pointed glass needles, groups of these so-called spores (cysts) or single thalli with their enclosed cysts were readily picked from the soil, rinsed several times in sterile water, and transferred singly to drops of water on the surface of nutrient agar in a petri dish. Several hours afterwards numerous zoospores were produced which were then transferred to further nutrient media. Repeated transfers in this manner, of the progeny of single thalli thus gave uni-algal cultures within several days. All fungi were eradicated from the cultures by these repeated transfers and growth of bacteria was very slow and negligible in effect. Detmer's nutrient medium in concentration of 1.75 grams per 1000, solidified with agar to a consistency of 2%, was used exclusively. Several separate isolations of the organism from different localities were made by the methods described above to determine whether or not there were any differences. For comparison cultures of *Protosiphon botryoides* were also secured from the Pflanzenphysiologisches Institut der deutschen Universität in Prague (Pringsheim 1929), and it was found that all forms isolated from different localities were identical with the European one. Cultures were grown on agar slants, in petri dishes and erlenmeyer flasks in a moist atmosphere and protected from direct sunlight.

For cytological studies the method employed by Schwarze (1922) in his study of the water molds was used. Material for fixation was grown on agar in petri dishes. Drops of fixative were placed on the plants with a pipette and subsequently, melted agar near the point of solidification was poured over the plants. The agar solidified almost immediately and small

blocks containing the algae were cut out and dropped into vials containing a large quantity of fixative. These agar blocks with the thalli were washed, dehydrated, imbedded and sectioned in the usual way. In this manner the plants which at certain stages do not adhere firmly to the substratum are prevented from floating off during washing and dehydration. Of a variety of fixatives Flemming's weaker solution and Allen and Wilson's modification of Bouin's fluid (Allen's B-15) produced the most satisfactory preparations. Sections were stained in Flemming's triple stain or in Haidenhein's iron haematoxylin. The former in general was more differential. A modification of the usual technique was employed with the free swimming zoospores. To slides coated with a thin film of egg albumin were added drops of water containing the motile cells. These were mixed with a small drop of Flemming's weaker fluid and allowed to evaporate. When the margin of the drop was quite dry, the slides were immersed in alcohol and stained in the same manner as sections.

CULTURAL CHARACTERS

When a group of plants is placed on the surface of freshly poured and cooled Detmer's agar, numerous zoospores are produced within a few hours and swarm radially for considerable distances from the point of inoculation, forming discoidal colonies where they come to rest. If the number of swimmers is large they form dense films whose individuals are angular except at the free surfaces. They are very sensitive to light variations and the shape of the young colony is to a large extent determined by light intensity, unilateral light producing asymmetrical colonies. The extent of the water film on the surface of the substratum determines the density and radius of the colony. As the zoospores develop their apices are lifted above the surface of the medium so that the rhizoidal portion alone is in contact with the substratum. This is true only for densely inoculated cultures where the plants are mutually supported. Isolated plants have the tendency to be more procumbent. The thalli in mature and crowded cultures may extend as high as several millimeters above the agar surface.

The color of the plant mass changes with age from a bright yellow-green, through green to dark olive green, and with the combination of bright light and low moisture-content of the medium, becomes bright brick red. Cultures from two to four weeks old have a shiny, glistening appearance, which later becomes dull and powdery due to the endogenous segmentation of the transparent thalli into numbers of dense and opaque cysts.

Observations of hundreds of cultures on solid media so far indicate that the first swarming period after inoculation, which may continue for several

consecutive days, is the only one until the plants are fully grown. This is perhaps due to the decreased moisture-content of the agar resulting from evaporation. Unless the plants are later submerged either by adding water or by droplets of condensing water vapor, no further multiplication is accomplished by zoospore formation. The water of condensation is often sufficient stimulus to initiate zoospore production, but unless it submerges the plants, the zoospore anlagen do not leave the parent thallus. Instead they develop walls and subsequently become new plants. Similar correlations between culture conditions and development were found in *Chlorococcum infusionum* (Bold, 1931). In addition to these inhibited zoospores cell multiplication is accomplished by separation of buds and lobes from young thalli by septa, as shown in figures 74 and 75. Growth on solid media is confined to the surface of the substratum, and in such cultures approximately one month is required for zoospores to develop into mature thalli.

THALLUS STRUCTURE

The *Protosiphon* thallus attains its best development on very moist soil cultures. Under such conditions the aerial portion of a single plant may extend half a millimeter above the surface of the substratum with the unbranched rhizoid penetrating the soil to a depth of a millimeter. The subterranean portion is quite colorless and contains a thin layer of protoplasm surrounding one continuous vacuole, or a series of central vacuoles. Chlorophyll is developed only in the aerial, bulbous portion of the plant.

Growth and development in agar cultures is only slightly inferior to that on soil. Under crowded conditions the aerial portion of young plants may become lobed and branched, and often such branches and buds are cut off from the parent plant by definite partitions as noted above. I have been unable so far to follow this process of septation because it occurs in agar cultures and as soon as the plants are placed in drop cultures either all development ceases (if the plants are young) or zoospore formation soon occurs. When a large number of individuals are growing together on a small surface the cell shape is generally narrower, and the bulbous portion tapers more gradually into the rhizoid.

The central region of the thallus is occupied by a large vacuole which may be continuous from the base of the rhizoid to the apex of the thallus or consist of several vacuoles separated by thin laminae of cytoplasm (figs. 69–75, text fig. 2). The primordial utricle extends deeply into the cell cavity in the bulbous, expanded portion of the thallus but nearer the rhizoid it becomes thinner and sometimes membranous (figs. 2, 3). From observation of living and stained preparations I have been unable to dis-

tinguish a differentiated chlorophyll-bearing region of the cytoplasm or definite chromatophore such as occurs in the cells of *Botrydium*, *Vaucheria*, *Nitella*, and the phanerogams. The chlorophyll completely pervades the cytoplasm of the upper portion of the cell and shades off imperceptibly into the colorless cytoplasm in the rhizoidal region. Further evidence for this is available from study of sectioned material, in which no distinction between colorless and chlorophyll-bearing cytoplasm is apparent (figs. 1, 25, 39, 40). Pyrenoids are present both in the peripheral and deeper protoplasm, and the nuclei are more or less evenly distributed between the plasma membrane and tonoplast. According to my observations the *Protosiphon* thallus is in this respect very similar to that of *Hydrodictyon* in which Timberlake (1901) reports the absence of a specially differentiated chromatophore though Klebs (1891) described a differentiated net-like chromatophore as he did also for *Protosiphon*.

In general the pyrenoid is surrounded by a number of starch grains which are evident in the living cells and stain typically with aqueous iodine-potassium iodide solution. Starch is most abundantly developed around the pyrenoid in thalli which are entering the encysted condition (figs. 6-10, 38, 39). In favorable preparations stained with the Flemming triple stain the pyrenoid appears a brilliant ruby red, while the surrounding halo of blue starch grains is imbedded in the orange tinted cytoplasm. While the pyrenoid is sometimes homogeneous and spherical, it more often appears either vacuolate or fissured and segmented as in figures 6-10. In such segmented pyrenoids the central and continuous mass of the body is typically ruby-red in color, while the peripheral segments which split off stain more opaquely and are of purplish-red tint. The starch grains surrounding the pyrenoid take up the gentian violet with avidity. A careful study of the staining reactions of the pyrenoid mass, the segments which split off from it and the enveloping starch grains, in addition to the relative position of the starch segments with respect to the pyrenoid itself, show that the fragments or portions of the pyrenoid which are separated from it become transformed into starch grains. In optical section the starch segments are parenthetic or wedge-shaped sectors; careful focusing shows that together they often form the surface of an incomplete, hollow sphere. In many preparations the pyrenoids are imbedded in a region which stains more heavily with Orange G than the general cytoplasm (fig. 1). It may be that in these regions the insoluble starch has been made available for metabolism by transformation into another form of carbohydrate, although I have found no evidence of hydrolysis of the peripheral starch segments which adjoin this orange-staining region. The relation of these observations to those of other investigators will be discussed later.

The mature thalli are always multinucleate, this condition arising very early in the development of the zoospore (figs. 19–23). The zoospore is uninucleate when liberated from the parent cell and after coming to rest, but the nucleus soon divides, forming a progressively larger number as the thallus develops. Unlike *Synchytrium* in which the vegetative thallus is uninucleate (Harper, 1899) until immediately before reproduction, the thallus of *Protosiphon* is coenocytic throughout its vegetative development. Klebs (1896) states that the nuclei are confined to the deeper, colorless cytoplasm, but I am convinced from study of sections (fig. 1, etc.) that they are evenly distributed between the vacuole and cell wall. Although small, the nuclei have an appearance strikingly like that of the higher plants (figs. 1, 11, 12, 25–28). With the Flemming triple stain usually a single red nucleolus and blue chromatin material are clearly visible within the nuclear membrane. The chromatin may be largely confined to the periphery of the nucleus (fig. 11), although more often it is distributed as a reticulum through the nuclear cavity (fig. 12). The view of Golenkin (1899) and others that in many algae the nucleus is of primitive organization with chromatin aggregated in the center in the form of a large karyosome nucleolus is not tenable in *Protosiphon* as far as my observations go; for in addition to the safranin-staining nucleolus a well developed chromatin reticulum is always present and the nucleole apparently plays no rôle in the formation of the chromosomes. I have so far not found a complete series of the successive stages of nuclear division, but the large number of isolated stages observed show clearly that the process is essentially similar to that in the higher plants so far as the formation of the chromosomes is concerned.

The chromatin of the resting nucleus during early prophase becomes spireme-like (figs. 13, 14) and is then segmented into a number of chromosomes which lie scattered in the nuclear cavity. Spindle fibers develop from both poles of the nucleus and the chromosomes become arranged at the equatorial plate (fig. 15). I have so far been unable to trace the origin of the spindle figure prior to the equatorial plate stage. At this phase the division figure lies within a clear zone and the spindle is distinctly bi-polar and stains violet in the triple stain. Study of a large number of nuclear division stages has convinced me that there is typically a centrosome present at each pole of the spindle (figs. 15, 16). In a great number of preparations the cytoplasm near the poles of the spindle is somewhat densely granular, but I have found no evidence of astral radiations. A great number of division figures are so oriented with respect to the plane of section that the poles are not plainly visible, and though the spindle fibers seem to converge, the centrosome in such figures does not appear at the pole. In more

favorable preparations there is a sharply red-staining granule at the point where the fibers converge. In certain preparations a single (fig. 14) or two (fig. 13) deeply staining bodies are visible on the nuclear membrane and may represent isolated stages of the division of the centrosome. The division figure is intra-nuclear (figs. 18, 15) at least to the equatorial plate stage, but with the subsequent elongation of the spindle in anaphases and telophases it is not so sharply delimited from the cytoplasm. As it elongates the spindle may become slightly curved. The chromosomes are densely aggregated when they reach the poles and from these groups the daughter nuclei are reorganized. In my preparations the chromosomes are very minute and densely crowded at the equatorial plate stage, and for this reason it is almost impossible to make an accurate count. In the most favorable preparations the number seems to be fairly large, and approximately twelve have been counted in several figures.

Synchrony of nuclear division in coenocytes and syncytia both in plants and animals has been often reported, and Karling (1928) has summarized the more important available data. He distinguishes between complete synchronism in which all the nuclei of one cell divide simultaneously and are in the same stage of division at the same time, and progressive synchronism in which division is simultaneous but the seriation of stages discontinuous. Nuclear division in thalli of *Protosiphon* belongs to the second category (fig. 18). This figure shows that all nuclei are dividing simultaneously, but those at the apex are in the anaphase condition while the remainder are in the equatorial plate stage. The nuclear divisions in the protospores at the conclusion of cleavage more nearly approach complete synchrony (fig. 34). In the thalli, while the nuclei at the apex of the sac may be further advanced in division than those at the rhizoidal region as in figure 18, the opposite relation also obtains; so that nuclei at the rhizoidal portion may be more advanced than those at the apex. Similar observations have been reported by Strasburger (1880), Soltwedel (1882) and Némec (1910) for the embryo sacs of angiosperms.

The protoplasm in developing thalli and young coenocysts is characteristically highly vacuolate (figs. 1, 4, 25-27, text fig. 2). The primordial utricle may be almost completely perforated with rather large vacuoles. In many cases these intra-utricular vacuoles appear to be bounded by rather definite membranes which show avidity for the violet of the triple stain (figs. 27, 4, 5). The protoplast is bounded both externally from the wall and internally from the central vacuole by rather sharply differentiated membranes which become conspicuous during cleavage (figs. 29, 32) or when slight shrinkage is caused by reagents (figs. 5, 5, a). Figure 5, a, represents a more highly magnified view of a small portion of the pri-

mordial utricule of the same cell shown in figure 5. The interior membrane or tonoplast which separates the protoplast from the vacuole has been separated from the protoplasm by the action of reagents, though some cytoplasm still adheres to it.

The cell wall in all stages with the exception of old cysts and zygotes is quite thin. It swells slightly and stains intensely blue when treated with sulphuric acid and iodine-potassium iodide solution, suggesting a cellulose composition. I have not secured any evidence of lamellation. In mature cysts maintained under conditions of drought the wall is markedly thickened.

LIFE HISTORY AND REPRODUCTION

My observations confirm those of Klebs as to the life history of *Proto-siphon*. Examination of the zoospores formed after the inoculation of a new culture shows many of them fusing in pairs (fig. 67), and a large number also coming to rest without conjugation. During the first twenty-four hours both fused and single zoospores tend to round up and develop walls. The zygotes and single zoospores cannot be distinguished from each other on the basis of size alone, since there is a wide range of variation in the size of the zoospores themselves. It is thus not uncommon to find a young zygote smaller in volume than a single zoospore. The zygote during the next forty-eight hours becomes irregular in shape, its wall thickens irregularly and the contents become dense and opaque (fig. 69a). I have frequently followed the complete development of the zoospore into the mature thallus and figures 69-73 illustrate some of the phases from daily study of developing cultures. These cultures were inoculated at 9:30 A.M. and by 12 noon were rapidly producing zoospores. Figure 67, i, shows young zygotes and zoospores from the culture at the evening of the first day. The zygotes show clearly two stigmas, and the presence of two pyrenoids is in many cases indicative of fusion, while the zoospores on the other hand possess but a single stigma. Twenty-four hours later (fig. 69, a) the zygotes have become rather opaque and their wall rather irregular. In the same interval the zoospores have become either equal or larger in size than the zygospores (fig. 69), have developed walls, and many of them have begun to change their shape by enlarging somewhat at one pole. The pyrenoids are quite conspicuous with a surrounding layer of starch segments, and in some cases have divided or seem to be dividing. The central vacuole increases in size and is separated from the enlarging pole by a thin layer of protoplasm. There is no sharp distinction between chlorophyll-bearing and colorless cytoplasm. On the following day the cells have become considerably larger (figs. 70, 71) and elongated and somewhat sac-shaped. In

subsequent development (figs. 72, 73) elongation and enlargement of the cells continue and the apical region expands and becomes bulb-like, until in several weeks most of the plants have attained the mature form. I can thus confirm Klebs' contention that the fusing gametes always form a dormant zygote and that the great majority of unfused zoospores can grow directly into new plants. The failure of Rostafinski and Woronin (1877) to observe any further development of the non-fusing zoospores of *Protosiphon* may be correlated with the abnormal conditions in liquid cultures of this organism, which they were employing.

As to the so-called green and red "spores," development is substantially as Klebs and the earlier authors described. Their use of the term "spore," however, for these bodies is unfortunate, for they should more accurately be called "cysts" or "coenocysts." It is well known from the literature of the Protozoa, fungi, and Myxomycetes that encystment stages represent merely a physiological response to a given set of environmental conditions that may appear during the life cycle of an organism, and should this set of environmental conditions not develop, encystment does not take place. De Bary (1887) expressed this conception in his use of the term cyst for those stages of the Myxomycetes which under unfavorable conditions are able to pass into a resting state and to return again to the actively motile phase, when favorable conditions prevail. If we extend the term "cyst" to the algae as apparently West (1916) has done, the red and green "spores" of *Protosiphon* should properly be called "coenocysts," to emphasize their multinucleate constitution. They represent portions of the thallus formed under conditions of drought which can again produce the thallus with the coming of increased moisture content of the substratum. If the coenocysts are placed in water, like the thalli they respond by producing zoospores.

As introductory to a detailed description of the formation and development of coenocysts, zoospores, cytokinesis and fusion of gametes I have illustrated in text figure 1 the life history of *Protosiphon* as observed in cultures. This diagram represents the alternate methods of development and is explained by the legend.

Encystment. As has been reported by all earlier students of *Protosiphon*, under conditions of drought and strong sunlight, the thallus protoplast becomes segmented into a number of spherical coenocysts (fig. 28), which if produced in sufficient numbers become angular by mutual contact and pressure. Their formation is distinctly progressive and may extend over a long period. For this reason it is rather difficult to follow the process in a single thallus, since the plants do not grow well in hanging drops of agar and soon form zoospores if transferred to water cultures for observation.

Figures 25 to 28, a, represent stages of encystment as they appear in

fixed and stained preparations. One or several furrows appear on the outer surface of the protoplast and cut into the cytoplasm in a somewhat curved path (figs. 25, 26). Originating from a point at the inner surface of the thallus wall a membrane projects into the furrow and follows its path through the cytoplasm. This membrane grows rapidly, keeping pace with the progressing cleft (fig. 26). The inner edge of the membrane is often thickened as if an excess of wall forming substance were collected there,

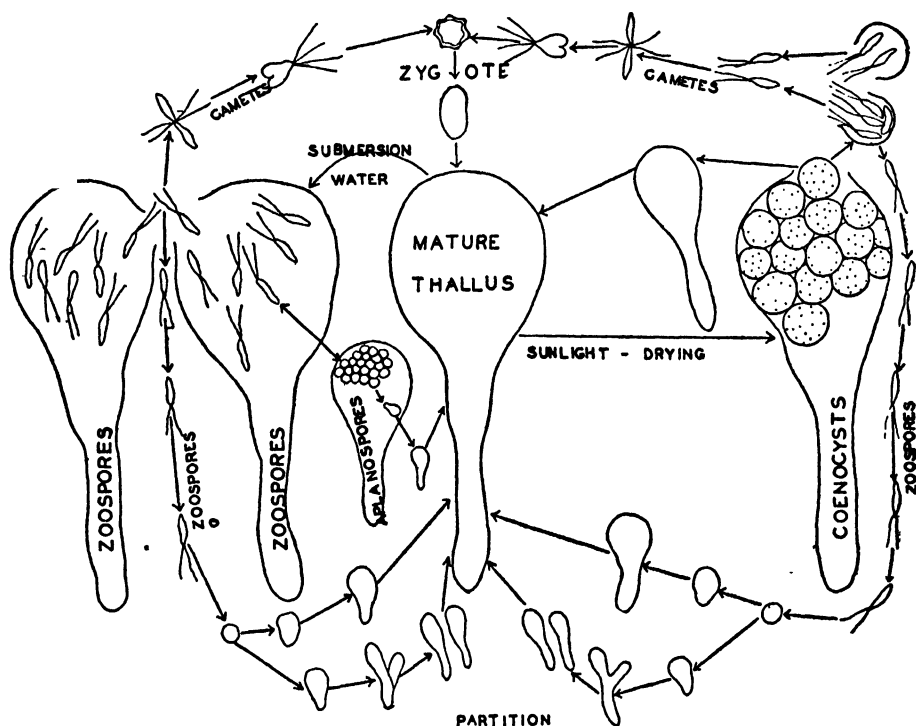


Fig. 1. Diagram of the life history of *Protosiphon botryoides*: thalli or coenocysts when submerged in water produce zoospores which may grow directly into thalli or fuse in pairs forming a zygote which germinates into a thallus after a period of dormancy. Thalli become segmented into coenocysts under conditions of drought and strong sunlight. (See text).

which stains purple in the triple stain. Furrow and membrane thus proceed isolating a portion of the cytoplasm and several nuclei (fig. 27). In large thalli the process is more progressive, larger portions of the protoplast being delimited at first and further subdivided into coenocysts (fig. 25). Although the membrane originates at the thallus wall its substance is doubtless augmented by formation of wall material by the protoplast on either surface of the furrow.

As the cysts are delimited from the thallus, their protoplasm is highly vacuolate, but as they mature the vacuoles gradually disappear and the cell lumen becomes completely filled with dense, granular protoplasm. This is clearly shown in figure 25, which represents a median section of a thallus undergoing encystment. Encystment of this thallus began at the apex near which the oldest and most mature coenocyst lies; its wall is thicker than that of the others and its protoplasm more dense. The coenocysts at the right of the apical one in the figure, were delimited subsequently and the highly vacuolate mass of protoplasm near the base is just undergoing further subdivision. When several pyrenoids are included in a single coenocyst they tend to collect in the center of the cell. After segmentation of the thallus protoplast is complete, the maturing cysts become densely packed and round off as far as possible (fig. 28). The number of nuclei included in the coenocyst does not increase subsequent to its formation. Mature coenocysts may be further sub-divided as shown in fig. 28. As the cells mature their walls become thickened. Coenocyst formation involves the protoplasm of the rhizoidal portion of the thallus (fig. 28a). This observation makes it questionable whether the basal portion of the thallus should be properly termed a rhizoid in view of Karling's (1932) report that true rhizoids play no role in multiplication of the thallus in the fungi.

Zoosporogenesis in the thallus. As has been noted above, Cienkowski (1855), Rostafinski and Woronin (1877) and Klebs (1896) describe the formation of zoospores from thalli growing on solid media when covered with water. This occurs in nature when the soil is saturated after heavy rains or floods. It has been my experience that swarmspore formation is the invariable response to submerging plants from agar cultures. It is usually difficult to secure zoospores from plants younger than twelve to fourteen days, but after this time almost every submerged thallus undergoes zoosporogenesis.

The following method was used for securing and studying zoospore formation: Large plants from month-old cultures were carefully removed from the agar and placed in hanging drop cultures of distilled water or dilute (.57%) Detmer's solution. At the same time the plants which remained in the culture were submerged to a depth of half a centimeter. The hanging drop mounts were retained under constant observation while thalli from the submerged agar cultures were periodically observed as a check on possible pathological conditions which might develop in the drop cultures.

A large number of thalli undergoing zoosporogenesis have been studied and the observations here reported are based on those of March 19, 1932.

Plants from a culture of February 18 were placed in hanging drops of distilled water and the plants remaining in the culture were submerged as described above. Several cultures were kept under observation simul-

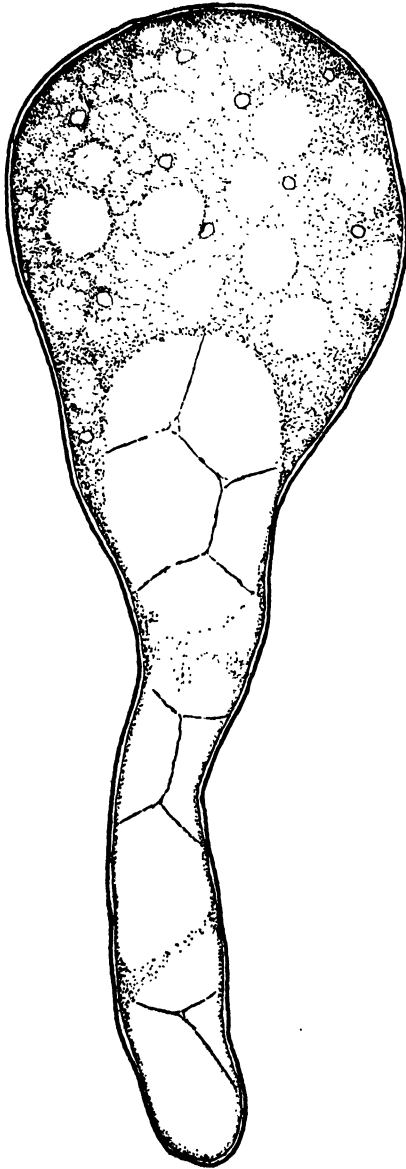


Fig. 2. Appearance of thallus immediately after submersion in water (11:45 A.M.).

taneously and although text figures 2, 3, and 4 are drawings of the same thallus at successive stages, they are typical of all thalli.

Text figure 2 illustrates the appearance of the thallus at 11:45 A.M. immediately after immersion in the hanging drop. Most of the protoplasm lies in the upper portion of the cell, while a thin peripheral layer extends over the inner surface of the wall toward the rhizoidal region. The chlorophyll is limited to the cytoplasm of the expanded region of the thallus leaving the basal region quite colorless. The chlorophyll-bearing cytoplasm is not sharply bounded from the colorless. At the cell base the protoplasmic layer or primordial utricle is extremely thin and the vacuole extends very close to the wall. The protoplasm at the apex of the cell is extremely spongy and vacuolate and the hyaline pyrenoids and numerous small oil droplets are conspicuous. The center of the cell is occupied by a large vacuole which in this particular cell is traversed and subdivided by strands of cytoplasm into several chambers of bubble-like appearance. This chambered condition of the central vacuole does not occur generally and has been only occasionally observed. Within thirty minutes the protoplast became less spongy and more densely granular. This change appeared to come about by the gradual excretion of the more aqueous phase of the protoplasm into the central vacuole, as evidenced by changes in the shape of the chambers, movements of their bounding membranes, and the appearance of oil droplets and granules in the previously optically empty vacuole. The protoplasm near the rhizoidal pole flowed gradually towards the apical region. By 2 P.M. the vacuolated regions in the protoplast were very much less evident, causing it to appear densely green and granular. Yet at this time the cell was still completely turgid. At 2:10 P.M. contraction began, the protoplast shrinking from the apical region of the cell wall, and at the same time the vacuole began to draw away from the base of the rhizoid. The pyrenoids were still visible at this stage but immediately after became obscured due to the increasing density of the chlorophyll-bearing cytoplasm. This increasing density is the result of further dehydration of the aqueous phase of the protoplast. Small vacuoles with refractive droplets were continually forming and bursting from the outer surface of the protoplasm as well as discharging into the central vacuole, or in some cases remained attached to the surface layers for some time. The formation and bursting of these surface vacuoles appears very similar but less rapid than the action of the contractile vacuoles described by Lloyd (1924, 1926 a, b) in the contraction of the gametes of *Spirogyra* prior to conjugation.

The contraction phase occupied two hours and was of relatively long duration compared with the other stages in cleavage. The extrusion of liquid from the surface of the protoplast and central vacuole continued as far as I could observe until 4 P.M. During this period there was constant

change in size and shape of the chambers of the central vacuole. By 4 P.M. the protoplast had shrunk to approximately one-third its original volume, and the central vacuole was but a small sac filled with numerous

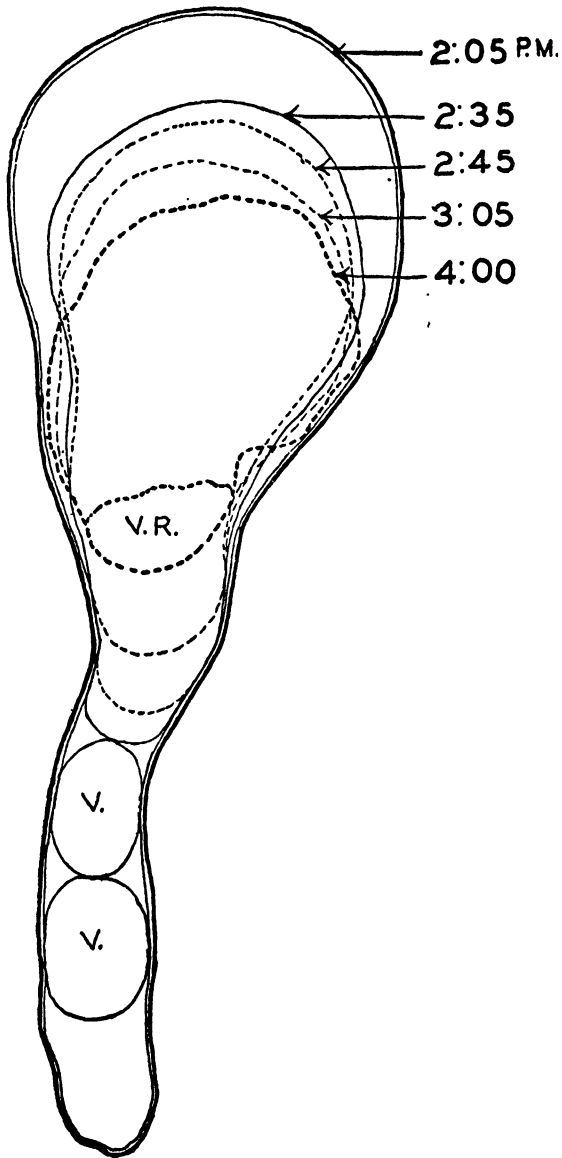


Fig. 3. Successive stages of contraction of the protoplast in thallus of fig. 2. (time intervals indicated). V.R. = vacuole remnant.

droplets and granules. Text figure 3 represents changes in the outline of the protoplast and its relation to the wall in optical section from the

initiation to the completion of contraction. The changes of position with reference to the cell wall during contraction become apparent from these diagrams. Of special interest is the relation of the plasma membrane to the wall during this gradual contraction. As the protoplast drew away there remained numerous fine hyaline threads running from the surface of the protoplast to the cell wall which persisted until the protoplast had shrunk to about one-half of its original volume. I have been unable to follow with certainty the fate of these threads in living cells but their presence here is highly suggestive of the observations reported by Chodat and Boubier (1888) that in slow, artificial plasmolysis of plant cells the plasma membrane remains connected to the wall by hyaline strands. The plasma membrane was very clearly visible as a double contoured structure during the contraction phases.

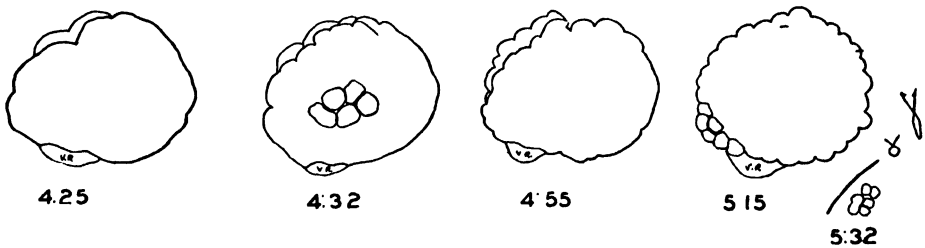


Fig. 4. Diagrams of zoosporogenesis by progressive cleavage in the same protoplast: (time intervals indicated).

From 4 to 4:10 P.M. no visible change of the protoplast occurred. At 4:10 P.M. the rounded contour of the protoplast began to change rapidly; the surface of the protoplast became slightly folded and lobed and in optical section the surface seemed to be invaginated at several places. Following this lobing more numerous delicate invaginations or furrows appeared over the surface. This process of furrowing began first at one pole of the cell and extended gradually over the entire surface (text fig. 4). The course of the furrows was irregular, curved and branched and they appeared as narrow, linear, hyaline areas traversing the dense protoplast. It was impossible to follow their course more deeply into the protoplasm because of its density. These furrows continued to extend and branch until they had delimited large blocks of cytoplasm. By 4:45 P.M. the entire surface was cut up into these large blocks which showed a slight tendency to polygonal outline. Careful focusing showed the formation of new furrows on the surface of these large blocks which by 5:25 P.M. had subdivided the protoplast into numerous small segments.

Then followed a period of slight swelling so that the surfaces of the re-

cently delimited segments became closely appressed and the lines of cleavage more difficult to follow. However, a study of the margin of the protoplast demonstrated that the latter was completely segmented. Superficial segments observed at this time appeared to be undergoing bipartition, a lighter hyaline area forming across the equator of each segment.

At 6:03 P.M. a slight gliding movement of the segments began which became gradually accelerated until they developed a quite rapid motion. At the beginning of the motile period none of the segments moved outside the original boundary of the contracted protoplast, but with the acceleration of motility they finally invaded the entire lumen of the thallus. As movement increased it changed from a slight local turning and gliding motion to a more active darting back and forth of the swarmspores. These motile segments which were first confined to within a short radius of their place of origin moved to greater distances away from it. I am at a loss to account for the tendency of the motile bodies to remain at the center of the thallus cavity for some time after motility has begun, since there is no sign of any gelatinous material or bounding membrane to hold them in position. The nature of their surfaces may possibly cause them to adhere to each other.

During this period of motility within the thallus the zoospores increased slightly in size and changed their shape from irregular ovoid to somewhat definitely heart-shaped and finally became quite elongated and spindle-shaped (text fig. 4). The first zoospores were liberated at 7:10 P.M. by a localized, apical, slightly lateral rupture of the mother wall. At first they escaped a few at a time and rather slowly as if they were passing through a gelatinous layer which inhibited rapid motion. The remaining individuals swam rapidly through the opening into the surrounding medium. Several were apparently unable to escape from cell lumen and continued their movement until observation ceased. The entire process of zoospore formation from the immersion of the cells in water to the liberation of the mature swarmspores occupied in this particular thallus seven and three quarter hours.

Although the above description applies in general to all cleaving cells of *Protophloea*, I have noted several slight modifications. In certain thalli during contraction the protoplast may become divided into two or several portions which are separate from each other but partly in contact with the central vacuole. In a very few cases cleavage appeared to begin before contraction became at all extensive. In such cases the protoplasm is more vacuolate and the furrows appear broader, some of them appearing to be almost of vacuolar nature. The period required for contraction and cleavage varies somewhat with the size of the cell, being in general more rapid

in the smaller thalli. This apparent correlation can be more advantageously discussed at the conclusion of the following section.

It is obvious from the above account that only the more general features of the cleavage process can be observed in living cells. For details month-old cultures were submerged in water and weak Detmer's solution and pieces of the agar with the plants were cut out and fixed at various time intervals, imbedded and sectioned at from five to ten microns as described above.

Such sections of cells which had been fixed immediately after immersion in water have the appearance of the one shown in figure 1, which is a slightly oblique section of a thallus. The rhizoidal portion of the cell here shown is completely filled with protoplasm but study of the consecutive sections demonstrated that this is largely due to the orientation of the thallus in such a manner that the plane of section cut through the periphery of the rhizoidal region and formed a more median section at the apex of the thallus. Median sections of the cell base (figs. 2, 3) show that the protoplasm normally consists of a thin parietal film between the wall and central vacuole. In the bulbous portion the primordial utricle is much thicker and the vacuole is much smaller in proportion to the volume of the cell cavity. The protoplasm is an extremely loose and spongy reticulum as in the living cells and the nuclei lie within its meshes. The number of nuclei in a cell of the size shown in figure 1 is very great in view of the fact that nuclei here figured consist only of those lying in a single plane of focus ten microns thick. The tonoplast is quite conspicuous as a thin blue-staining membrane between the vacuole and protoplast and the plasma membrane stains in similar fashion.

Although some plasmolysis occurs in fixation it can be readily distinguished from the shrinkage which occurs in preparation for cleavage. In the latter the protoplasmic reticulum is less open, while in the former the shrinkage is apparently confined to slight loss of water from the central vacuole, leaving the remainder of the protoplasmic structure unaffected. The suggestion based on observation of living cells that shrinkage is accomplished by extrusion of water and droplets of material from the protoplast into the central vacuole as well as from the periphery is readily confirmed in the study of fixed sections (figs. 29, 31, 32). Many such preparations show that material is accumulating in the central vacuole near the tonoplast and that vacuoles are forming and bursting at the surface. Some of this material is in the form of droplets, while in many cases there is also an abundance of numerous small granules which have great avidity for gentian violet.

During contraction the plasma membrane is conspicuous (figs. 29-31).

In the most favorable preparations it stains deeply with gentian violet and is clearly distinguishable from the deeper cytoplasm which shows affinity for Orange G. As soon as contraction of the protoplast has been completed cleavage begins. Division of the protoplasm is clearly accomplished by a process of progressive cleavage by furrows and not by either successive bipartition or so-called simultaneous multipartition by precipitation of membranes between the nuclei. This fact becomes very obvious from examination of preparations such as those figured in 29-32, 29 and 31 being cross sections through the contracted protoplast at right angles to the long axis of the thallus, while 32 represents a slightly oblique section. Only a portion of the thallus wall is shown in these figures but it is nonetheless sufficient to indicate the extensive shrinkage of the protoplasm. The cavity between the wall and surface of the spore plasm is completely void of any stainable material and appears as an optically empty region even in the most densely stained preparations. The only exception to this statement is the occasional occurrence of droplets and granules between the wall and protoplast, presumably secreted by the latter (fig. 37).

The furrows may begin either internally from the surface of the vacuole or at the periphery by invagination of the plasma membrane (fig. 29). From the study of successive stages of the process it becomes evident that furrows may also appear in the deeper protoplasm simultaneously with surface furrows. These more deeply lying furrows appear to terminate abruptly and are not continuous with those from the surface. These later clefts are open and broad at the surfaces but narrow as they cut deeper into the protoplasm and have sharp edges. As noted by Harper, there is no visible differentiation of the protoplasm in the path of the progressing cleavage furrow. The furrows cut through the spore plasm at varying angles and with curved paths at first with no apparent relation to the nuclei or to each other. Usually from the initiation of the contraction stage to the completion of cleavage no nuclear divisions take place (figs. 29-33).

As emphasized in the study of living cells, the surface furrows may form and progress more rapidly in one region than in others as shown in figure 29. This figure illustrates clearly the tendency for furrows from the vacuolar surface to fuse with centripetal radial furrows from the plasma membrane as is the case in *Didymium*. By the gradual coalescence of these and further tangential clefts large irregular multinucleate masses are cut out as illustrated in figures 29, 31, 32. Furrows then appear on the surfaces of these multinucleate blocks which are finally divided into uninucleate segments as shown in figure 33. During these final stages of cleavage the nuclei tend to lie near the path of the cleavage furrows.

These segments are relatively small and numerous and closely ap-

pressed as shown in figure 33, which represents a small portion of a section. The more central segments are often more polygonal in shape than the peripheral ones. The single nucleus is in the resting stage which is typical during the entire cleavage process (fig. 30). Although in many cases the uninucleate segments are closely appressed, it is not very difficult to observe the clefts between them; these segments are destitute of cell walls and are bounded merely by their plasma membranes.

The cleavage segments do not become motile immediately after their formation, and they are not definitive swarmspores, swarmspore-initials or swarmspore anlagen. As far as my observations go they will under no circumstances develop flagella and function as swarmspores. In the discussion of the process in living cells evidence of a bi-partition of the end products of cleavage was pointed out. This occurs before motility is initiated. Study of stained sections confirms this observation. The single nucleus of every segment undergoes division (fig. 34) which is then followed by bipartition of the segment (fig. 35, 36). The nuclei of the segments throughout the entire thallus divide with almost complete synchrony. Cell division is accomplished by the formation of a lighter staining zone across the equator of the now bi-nucleate segments (fig. 36), through which constriction takes place. I am still uncertain as to whether one or two nuclear and cell divisions occur in the uninucleate protoplasts. An attempt to secure indirect evidence on this question by measuring the relative sizes of the constricting segments, and comparing them with the initial uni-nucleate protoplasts was abandoned because of the great variation in the size of the original segments themselves. The question as to whether more than one division regularly occurs thus remains unsettled. At the conclusion of the final bi-partition the segments withdraw somewhat from each other, increase slightly in size and develop into swarmspores.

The nucleus enlarges slightly and takes up a peripheral position so that the nuclear membrane is in close proximity to the plasma membrane (fig. 46) of the zoospore initial. Immediately after this stage there appears a deeply staining granule between the nucleus and the plasma membrane from which the flagella develop (figs. 37, 45, 46). I have been unable to trace the exact origin of this granule. It always arises in close association with the nucleus and is unquestionably the basal body or blepharoplast from which the flagella are organized. Its close association with the nucleus suggests the possibility that it may have been derived from the centrosomes which are present at the poles of the spindle figure.

Shortly following this stage the zoospore initials separate, doubtless as a result of the motility described above in living material, and their slight

increase in size and change in shape can be readily followed in the sectioned material (figs. 37, 45-47). In free swimming zoospores (figs. 47, 53) the nucleus lies near the apex and slightly withdrawn from the plasma membrane. In favorable preparations it is clearly seen to be connected to the basal body by a delicate protoplasmic fiber or strand (rhizoplast). The chromatin appears more condensed in the nuclei of the free swimming zoospores but it is possible that this is only the result of the method of preparation. The stigma does not stain clearly. In some of the zoospores one or several small pyrenoids are present in the posterior region, while others lack them (figs. 67, 68).

As to the behavior and development of the pyrenoid during zoosporogenesis there is some variation. In living cells it soon becomes obscured by the increasing density of the protoplasm, while in stained preparations it sometimes appears to break down into smaller fragments (figs. 29, 31), which may be disseminated through the cleaving cytoplasm or remain collected in clear areas (fig. 31). In other cases no trace of fragments can be found (fig. 32) and the pyrenoid loses its affinity for the stain, leaving a clear area in the cytoplasm. In the former case most of the zoospores receive one or more of the red staining fragments during cleavage, while others lack them entirely. When the pyrenoid entirely disappears new ones arise *de novo* in the zoospores after they have come to rest. This is quite evident from living zoospores (figs. 67, 68), some of which have pyrenoids and others not. The data on the question of the inheritance of the pyrenoid has been summarized in a previous paper (Bold, 1931); pyrenoid behavior in *Protosiphon* is similar to that described by Miss Carter (1926) for members of the Ulvaceae. The contractile vacuoles in well fixed preparations appear as clear areas at the anterior extremity of the cell (figs. 47, 53).

Zoosporogenesis in coenocysts. Zoospore formation has been repeatedly observed in both green and red coenocysts of *Protosiphon* after removing them from agar cultures or soil to drops of liquid media as in the case of the thalli. Text figures 5, 6, and 7 are diagrams of this process as it occurs in living cells. In all essentials it is similar to that described in the thalli. In young coenocysts with vacuolated protoplasm the protoplast becomes denser and collects at one side of the vacuole (text fig. 5) by the progressive excretion of water, droplets, and granules into this latter region. As the protoplasm extrudes water its vacuolate appearance changes and the pyrenoid becomes obscured with the increase in density. Loss of water from the protoplast and central vacuole continues until the volume of the protoplast has greatly decreased (text fig. 5). When contraction has reached a certain point segmentation is initiated. It is accomplished by invaginations or surface furrows which grow and branch, isolating some-

what irregular masses of protoplasm. These are in turn sub-divided by secondary furrows on their surfaces into still smaller portions. As in the case of the mature thalli these segments swell slightly, become closely appressed, and remain in this condition for a short time. Finally they undergo either one or two bipartitions, so that there are formed in the coenocyst cavity a number of small protoplasts. These round off and develop flagella. A feeble gliding movement becomes evident and is gradually increased until the swarmspores are swimming rapidly through the cavity of the coenocyst. They are liberated by rupture of the wall and swim away

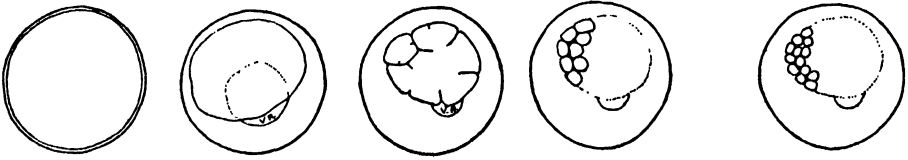


Fig. 5. Diagrams of zoosporogenesis in immature, vacuolate coenocysts.

into the culture medium. I have not so far observed the occasional liberation of zoospores in a gelatinous vesicle which Klebs figures; however, this method of escape is not universal as he has pointed out. The central vacuole often remains within the empty cell as a small hyaline sphere, which indicates a well differentiated and persistent tonoplast.

In more mature coenocysts in which the central vacuole has disappeared entirely and whose cell cavity is completely filled with dense protoplasm, cleavage is more rapid, and practically no shrinkage occurs

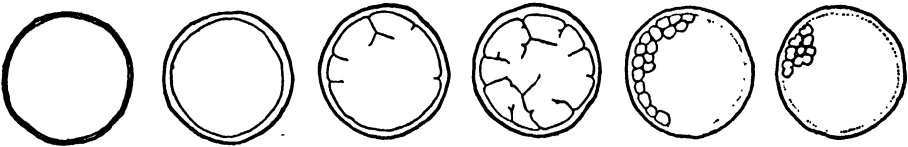


Fig. 6. Diagrams of zoosporogenesis in mature coenocysts with dense protoplasm in which the central vacuole has disappeared.

(text fig. 6, figs. 40, 43, 44, 48). Very soon after immersion in water furrows are formed at the surface of such cysts which quickly separate the protoplast into large segments which are subsequently divided into smaller portions. The final bipartitions take place as in the vacuolated cysts. The process of cleavage is thus the same in young vacuolated coenocysts as in the older, densely filled cells with the exception that it is more rapid in the latter type and a larger number of zoospores are produced in proportion to the cyst size.

I have already described the formation and structure of the coenocysts as they appear in sectioned and stained material. In younger cysts as in

the thalli the protoplast is spongy and vacuolate (figs. 38, 39) but during zoospore formation liquid is extruded into the central vacuole and it therefore becomes denser in appearance. In fixed and stained preparations it is apparent that the contraction stages are due first to the extrusion of water and other materials into the central vacuole and from the surface of the protoplast, and secondly to the decrease in volume of the vacuole itself (fig. 41). Except in the smallest cysts and aplanospores segmentation is invariably a process of progressive cleavage. When contraction is completed furrows appear in the protoplasm. In larger coenocysts the furrows may appear earlier at one pole than at the other so that cleavage may progress more rapidly in one part of the cell than in the other. Later clefts form in the deeper cytoplasm. They are usually broader at the surface and thin out at their edges (figs. 41–43). They curve and fork in various directions and as they come together isolate small multinucleate regions of the protoplast. In small coenocysts (text fig. 7) the primary furrows delimit

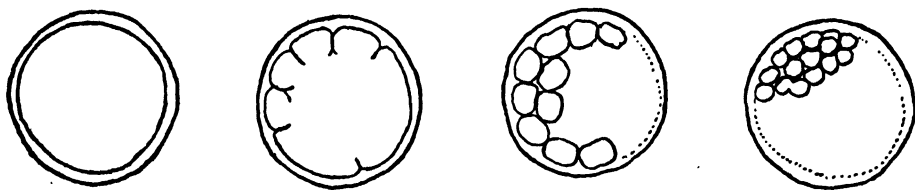


Fig. 7. Diagrams of zoosporogenesis in small coenocysts in which the primary cleavage furrows delimit uninucleate protospores directly.

uninucleate segments directly (fig. 43). In larger cysts when the multinucleate segments have been formed they are also sub-divided by furrows so that the protoplast of the coenocyst is transformed into a number of uninucleate segments. During the final cleavage stages the nuclei lie very near the cleavage planes and usually retain this position during the further development of the uninucleate segments (fig. 44). As in the thalli these uninucleate segments are not the zoospore initials or anlagen. After a period of slight swelling the single nucleus divides either once or twice (figs. 48, 51) and then follow one or two bi-partitions (fig. 50), the products of which become the zoospores directly and without further division. These segments round off somewhat and a blepharoplast appears near the plasma membrane from which the two flagella develop. When they first become motile they increase slightly in size and are globose, but as their movement is accelerated they become spindle-shaped (fig. 47). They are liberated by rupture of the coenocyst wall.

The process of cleavage is the same in both red and green coenocysts whether newly formed or mature, with the exception that in mature cysts

it is more rapid and there is very little contraction (figs. 40-44, and text fig. 6). In small cysts with few nuclei the process is similar but abbreviated (text fig. 7)

As the cysts vary in size they vary in the number of zoospores they produce. I have so far not observed the escape of less than four zoospores from a single coenocyst and this happens only occasionally. Usually the number is larger and in those cysts whose zoospores I counted carefully the number was almost invariably a multiple of two, presumably as a result of the final bipartitions

Structure and further development of the zoospores. When a large number of thalli and coenocysts of varying stages of maturity are placed in water, myriads of zoospores are produced within several hours and continue to be liberated for periods as long as several days. Liquid cultures thus become actually turbid with the swarms of zoospores which are positively aero- and phototactic, collecting on the surface of the medium nearest the source of light. If such a culture is rotated 180° with reference to the light source the zoospores move in a dense green cloud back towards the light. Motility appears to be more rapid in bright light than in the dark.

The zoospores are somewhat variable in both size and shape (figs. 67, 68). A few attain the length of 11 microns while the majority vary between 3 and 6 microns. When first liberated they may be somewhat globose, but as they swim about they gradually become elongated and spindle-shaped and in end view (fig. 68, a) appear round. Both ends are often colorless and pointed and a hyaline droplet is occasionally attached to the posterior end (fig. 47). The chlorophyll may extend to the posterior end but the anterior portion is always hyaline. In the living cells the blepharoplast with the two attached flagella can be quite clearly distinguished. The flagella are approximately as long as or slightly longer than the length of the cell body and beat very rapidly in propelling the zoospore. A minute pyrenoid may or may not be present but all zoospores contain a red eye spot which is imbedded in the green portion of the cytoplasm near the anterior margin. Two contractile vacuoles lie immediately below the blepharoplast. There is no conspicuous, definite cell boundary in addition to the plasma membrane. The plasticity of the zoospores becomes apparent when they collide with each other or force their way between other cells. They tend to collect near the margin of hanging drops and as they come to rest other zoospores swim towards the margin and force their way between them, and as this continues they become angular by mutual compression and contact (fig. 67, i). This occurs also on solid media and in such cultures the zoospores continue to develop so that

that pole of the cell not in contact with the substratum begins to enlarge in a direction perpendicular to the surface of the culture medium. In densely inoculated cultures as a result of the aggregation of the zoospores the bulbous aerial portion of the thallus becomes more slender and tapering (fig. 4). I have described previously (1931) a similar aggregation of the swarmspores as they come to rest in *Chlorococcum infusionum*. The polyhedral cell shape which is assumed in this organism, as the zoospores settle in crowded groups, is more permanent, resulting in loose coenobia of angular individuals, but isolated cells develop the spherical shape. In *Limnodictyon Roemerianum* Ktze. on the other hand (which is apparently closely related to *Chlorococcum*) this polyhedral shape, presumably acquired in the same way, has become fixed, since the cells of this species do not resume the spherical shape even when separated from the coenobium, as they do in *Chlorococcum*. In my first paper I suggested that the regularly constructed coenobia of *Hydrodictyon* and *Pediastrum* species may have developed from some such simple type of aggregation as occurs in these genera, and it is significant to note that Jost (1930) reports that isolated zoospores, mechanically freed from the *Hydrodictyon* mother cell, tend to develop the cylindrical cell shape when lying free in the culture medium.

Among the large numbers of zoospores liberated from cultures submerged in water many conjugating pairs are readily visible (fig. 67). In the process of fusion two individuals approach and become entangled with their flagella. They may swim around in this way for long periods (more than an hour) and finally separate. More often, however, when two zoospores become attached they begin to fuse at the anterior ends. In most of the cases observed the process occupies about one hour, and during this period the fusing pair continues motile. As far as can be determined in the living, motile cells, fusion begins at the anterior point where the blepharoplasts lie (67, a) and as it continues the cells appear to bend around toward each other (67, c-f), fusion proceeding gradually from the anterior to the posterior end. The completely fused gametes may continue motile for a short time and during this period they exhibit the same positive phototactic and aerotactic responses as the zoospores, intermingling with the latter at the margin of the drop (fig. 67, i). The outlines of the individual fused protoplasts are still distinct for some time after the zygote has come to rest and the stigmas and contractile vacuoles are present in double number, but eventually disappear (figs. 67, g, i).

The conjugation of zoospores has also been followed in fixed and stained preparations and the process is illustrated in figures 53 to 61. The gametes first come in contact at their anterior poles in the vicinity of the blepharoplasts (fig. 53) in the manner described for living material. Fusion is thus

accomplished by gradual coalescence along the adjacent lateral surfaces of the two individuals beginning at the anterior and extending progressively toward the posterior pole. The two nuclei retain their position near the blepharoplasts and may sometimes be in contact, while the blepharoplasts are very closely appressed and often appear as a single bi-lobed structure (figs. 54, 57, 58). After coming to rest the zygote becomes more spherical and the nuclei appear to lie nearer the center.

It is obviously impossible to follow the complete process of gamete fusion in the same individual pair in fixed and stained material, but some data have nonetheless been obtained on the length of time required for this process. A large number of thalli and cysts were placed in a small vial of water and carefully examined from time to time. Immediately after the first gametes and zoospores appeared near the surface of the medium fixations were made repeatedly at hourly intervals. The preparations fixed during the first two hours showed no zygotes with fusing nuclei, but did show many which had come to rest and whose nuclei were still separate. Material fixed during the third hour contained a majority of zygotes in which the nuclei were still separate, but in a few the nuclei were fusing or had fused completely. Preparations during the fourth and subsequent hours contained numerous zygotes in which nuclear fusion was taking place or had been completed. Such data are of course not specific for individual zygotes but nevertheless suggest that nuclear fusion in general takes place between three and four hours after liberation of the gametes and their plasmogamy.

The preparations of fusing gametes were made by the smear method and stained with haematoxylin and the triple stain; although nuclear details are quite clearly preserved the cytoplasm tends to stain densely, making it difficult to follow the fate of the blepharoplasts and flagella. In syngamy the nuclei come to lie in contact in the more central cytoplasm (fig. 59). They appear to enlarge slightly before fusion but in contrast to the nuclei of the free swimming zoospores they do not stain densely. The nucleoles are clearly differentiated and the chromatin is distributed in the form of delicate strands within the nuclear cavity. The nuclear membrane eventually disappears between the two nuclei and fusion takes place (fig. 60). The zygote nucleus is approximately double the size of the gamete nucleus and for some time later the two nucleoli remain distinct, while the chromatin contributed by each gamete nucleus becomes indistinguishably dispersed through the nuclear lumen. The two nucleoli often persist during the dormant period of the zygospore (fig. 62). The nucleus of the dormant zygospore is similar in position and structure to that in the young ones. Although I have so far been unable to follow definitely the

fate of the blepharoplasts in the zygote because of the density of the cytoplasm, some preparations occasionally showed rather deeply stained granular material in contact with the nuclear membrane (fig. 60) and it is possible that this is the remnant of the blepharoplast. The fate of the flagella in zygotes and zoospores could be readily traced in living cells. In either case they do not drop off immediately but continue to beat feebly for a short time. With this feeble beating they become gradually shorter and are then withdrawn into the cell. I have not succeeded in differentiating them after they are withdrawn into the cells in fixed preparations, but my observations of living cells convince me that they are not sloughed off but drawn back into the protoplasm (fig. 67, g-i).

In spite of the variation in size of the zoospores it is impossible to find any marked tendency for the larger gametes to conjugate with the smaller. Instead it has been my observation that the gametes which fuse are more often of similar size, large zoospores fusing in pairs as often as small ones. However, some cases of large gametes conjugating with small have been found (fig. 67, b).

Miss Carter (1926) in a footnote (p. 682) has noted that the gametes of *Protosiphon* will fuse and form zygotes within the same cell before they are liberated. Klebs (1896) on the other hand states: "Dagegen konnte ich noch feststellen, dass die Schwärmer der gleichen Mutterzelle nicht miteinander kopulieren." In view of the recent accounts of Hartmann (1929), Föyn (1929), and Gross (1931) of heterothallism among the Chlorophyceae and Schussnig's (1930, 1931) report of sex chromosomes in *Cladophora*, careful attention has been paid to this point in my study of *Protosiphon*. Numerous single thalli were removed from agar and placed singly in hanging drops to secure swarmspore formation. In a similar way single thalli which had formed coenocysts were isolated in hanging drops and finally single coenocysts themselves. In such single-thallus and -coenocyst cultures I have so far not observed the fusion of two zoospores. Two individuals may become attached for some time but finally they separate, and develop directly into new plants when placed on nutrient agar. In contrast conjugation is widespread in cultures containing numerous thalli. As noted above it often happens that several zoospores fail to escape from the thallus wall after zoosporogenesis and remain in the parent cell, come to rest and begin to develop. In examining many such thalli I have occasionally found a single star-shaped zygospor within the old thallus wall. Miss Carter's conclusion that *Protosiphon* is "monoecious" was based on the discovery of fusing isogametes within the same thallus resulting in typical zygospor. Klebs reports a few similar observations. Although such cases undoubtedly occur, my observations agree with Klebs' and indi-

cate that as a general rule gametes from the same thallus or coenocyst do not fuse with each other. I have so far obtained no conclusive evidence to affirm or deny the existence of genotypic differences in the gametes of *Protosiphon* and the cells which produce them.

Germination of the zygospore. As has been noted above the zygospore undergoes a period of dormancy. When a number of zygospores are transferred from an old, dry culture to fresh media their contents swell and the thickening of the walls becomes less apparent as the cells increase in size. After the cell size has increased somewhat and the zygotes have become more regular in outline, their growth is greater along a single axis and they soon become sac shaped and germinate into typical thalli. As yet I have not secured a complete series of fixed preparations of the germination of zygospores but certain stages appear significant. As the protoplast swells the single nucleus which has remained in the "resting" condition during dormancy, increases in size and the chromatin becomes aggregated into rather thick masses unevenly distributed within the nuclear cavity (figs. 63, 64). Subsequently some of the zygospores become binucleate (fig. 65) and finally tetra-nucleate (fig. 66). In the majority of cases by the time the tetra-nucleate stage is reached the contour of the cell is quite smooth. The nuclei continue to divide and the cell increases in size, eventually assuming the typical shape of the thallus. On the basis of these observations of the nuclear changes in the germinating zygote it is not yet certain whether or not reduction takes place. Too many of the intermediate and critical stages such as synapsis, diakinesis and careful chromosome counts are lacking to definitely answer this question. One might draw an analogy on the basis of the evidence at hand with conditions described by Miss Gross (1931) in *Ulothrix* and Allen (1905) in *Coleochaete* and suggest that reduction may occur in the germination of the zygote, but the evidence so far obtained is insufficient. A further report bearing on this question will be published as soon as more conclusive evidence is obtained.

DISCUSSION

As early as 1858 DeBary reported in his "Untersuchungen über die Familie der Conjugaten" that starch grains were present around the pyrenoids in *Spirogyra*. The association of starch grain formation with pyrenoids was emphasized by Schmitz (1882) who was the first to use the term pyrenoid. It has since been observed by many investigators, but it remained for Timberlake (1901) to demonstrate by refined staining technique that the large number of small autochthonous¹ starch grains in the

¹ Term first used by Wiesner (1900).

cytoplasm of *Hydrodictyon* cells are but transformed segments of the pyrenoid body, which have been split off from the latter and then been pushed out into the cytoplasm. The pyrenoids were commonly described and figured as spherical but in many cases they appear markedly polygonal in section as noted by Meyer (1883) in *Spirogyra*; this shape was not however viewed as related to the formation of the surrounding starch bodies by the earlier investigators. Timberlake showed that this characteristic sectorial contour came about by the splitting off of successive tangential segments from the mass of the pyrenoid which were gradually changed into typical starch grains. According to his account the transformation of such proteinaceous pyrenoid sectors into starch is accompanied by successive changes in staining reaction as the segments are pushed further out into the cytoplasm. Progressing centrifugally from the pyrenoid to the outermost segments in the cytoplasm, Timberlake described a gradual, transitional staining reaction from red, to gray, to purple, and finally to blue. The outlying segments stain characteristically blue in gentian violet and give the typical starch reaction with iodine.

Since the publication of Timberlake's observations several papers have appeared on the relation of the pyrenoid to photosynthesis in algae. Lutman (1910) in his study of *Closterium* found a single layer of large starch grains surrounding the pyrenoid in the form of a hollow sphere. Although the pyrenoid body was often much cracked and in some cases in planes which corresponded to the spaces between the starch grains, Lutman found no convincing evidence of the direct transformation of the pyrenoid segments into starch grains, such as Timberlake found in *Hydrodictyon*. McAllister (1914) and more recently his student Miss Ma (1931a, b) in their studies of the "multiple pyrenoids"² of *Anthoceros*, *Selaginella* and certain mosses have discovered that the elements of these pyrenoids show a change in their staining reaction successively from the center outward from brilliant red to purple to blue when treated with the Flemming triple stain, and they come to the conclusion that the elements of the multiple pyrenoid are the primordia of the starch grains. From my observations of *Chlorococcum* (1931) it appears that segments are cut off from the pyrenoid, become dissolved in the hyaline zone and subsequently starch is deposited in the cytoplasm surrounding the hyaline zone. On the other hand Bourquin (1917) reports that in *Zygnema* starch is formed at the periphery of the chloroplast without visible relation to the pyrenoid.

Study of the pyrenoids and their relation to starch formation in *Proto-*

² Term first used by McAllister (1914) to describe the compound condition of the pyrenoid in *Anthoceros*.

siphon leaves no room for doubt that the process is essentially similar to that which Timberlake described in *Hydrodictyon*. In *Protosiphon* the pyrenoid body stains brilliantly with safranin and surface segments separate from it. Both before and after they have completely separated they tend to stain a reddish-purple color, staining more densely than the pyrenoid itself, and as they move out into the cytoplasm they are transformed into typical blue-staining starch grains. Thus there is further evidence in *Protosiphon* for the view that starch formation at least in forms with pyrenoids involves the chemical dissociation of protein pyrenoid material into the carbohydrate starch. That a similar relation between protein and starch may exist in organisms without pyrenoids is suggested by the cytological work of Ma (1931b) on mosses, and by the chemical work of Samec and Haerdtl (1920) and Taylor and Walton (1929). Their report of the presence of phosphorus in starch has never been adequately explained on the current theory as supported by Willstätter and others that starch is the direct product of a synthesis of carbon dioxide and water, through such stages as formaldehyde and sugars. In addition Taylor and Nelson (1920) report the presence of nitrogen in the starch grains of the higher plants.

In relation to current theories, Baly, Heilbron, and Barker (1921) report the formation of formaldehyde from aqueous carbon dioxide solutions in light of short wave lengths, and the formation of sugars from formaldehyde in visible light when suitable photocatalysts were employed, and on the basis of their experiments suggest that the process of photosynthesis as it occurs in the green plant is largely dependent on the efficiency of chlorophyll as a photocatalyst. In accordance with such views it is generally assumed that the typical plant metabolism, like that of animals, consists essentially in the breaking up of complex carbohydrates as sources of the energy involved in the vital processes, the photosynthetic process being regarded as a preliminary, and as it were, an extraneous manufacturing of food materials.

There is no adequate explanation, however, on the basis of current theories of photosynthesis, for the observed fact that in organisms having chloroplasts with pyrenoids, photosynthesis involves a transformation of protein into starch or possibly sugars. Observation of the method of starch formation in such forms suggests rather that carbohydrate formation is a phase of the anabolic processes, involved directly in the building of the protoplasm of the green plant. The relation of the pyrenoid to starch formation suggests that the latter is in reality a storage product and that the protein of the pyrenoid is first formed as an excess in the general anabolic synthesis of food salts, carbon dioxide, and water into protoplasm. Starch

is subsequently formed as a storage product by the dissociation of the protein of the pyrenoid. The view that starch is a dissociation product of the proteinaceous pyrenoid is in harmony with Vines' (1886) theory of photosynthesis in the higher plants, which he compares with Strasburger's (1882) view that the cell wall arises by the transformation of peripheral protoplasm into wall substance. Vines maintains that photosynthesis involves the constructive metabolism (anabolic phase) of protoplasm, and that starch is to be regarded as a temporary reserve material formed as a dissociation product of protoplasm after protoplasmic synthesis has taken place. Vines emphasizes in his theory (thus deviating from current theories), the intimate chemical relation of the constructive metabolism of protoplasm with photosynthesis. His theory is supported by the data of Spoehr and McGee (1923) who found a close correlation between the rate of photosynthesis and the rate of respiration of lighted plants, so that decreased supply of carbohydrates in the leaf results in decrease in both photosynthesis and respiration. In this connection a statement of Miller (1931, p. 440) is significant in which he says: "In regard to the question concerning the first sugar formed in photosynthesis, an observation of Miller (1924) is worthy of note. He found that the total increase in the dry matter of the leaves during the day could not be accounted for by the increase in the sugars and insoluble carbohydrates during the same period. The increase in the total sugars and insoluble carbohydrates in the leaves during the day approximated only from 46 to 92 per cent of the total increase in the dry weight of the leaves for the same period. Since the cellulose content of the leaves did not increase during that period, it would appear that certain compounds were being formed which are not detected by the methods of carbohydrate determination as now used."

Coenocyst formation in *Protosiphon* is strikingly similar to cytokinesis in many other algae. *Cladophora* has long been a favorite object for the study of cell division. As early as 1835 Winter, and later Von Mohl (1845) described and figured quite accurately cell division in *Cladophora* (*Conferva*) *glomerata*, by a so-called ingrowth of a ring-like partition from the wall, which divided the protoplast of the mother cell, and thus for the first time proved that cells arise by division from pre-existing cells. On both surfaces of this partition the daughter cells secrete a new wall. Brand (1908) has recently confirmed these observations of cytokinesis in *Cladophora*. By treating the filaments with acetic and sulphuric acids he has distinguished several layers in the wall. The entire filament is surrounded by a continuous gelatinous sheath, within which lies the cell wall, which in turn is divided into an inner and outer layer, the inner layer being in contact with the plasma membrane. At cytokinesis the protoplast is pushed

back slightly from the wall at the point where division is to take place due to the gelatinization of the wall at that point. From the surface of the inner layer a ring-like cross wall develops and is deposited centripetally thus dividing the protoplast. The ring-like wall develops from within the inner wall layer so that the latter keeps pace with its growth and forms the end walls of the daughter cells. Such a stage as my figure 25 of *Protosiphon* is similar to the figures of Von Mohl and Brand of cytokinesis in *Cladophora*. The secretion of wall material into the furrow, continuous with the inner surface of the thallus wall is an essentially similar process in *Protosiphon* and *Cladophora* and in both cases takes place without relation to the position of and to the time of division of the nuclei. Lutman (1911) describes and figures cytokinesis in *Closterium* by the ingrowth of wall substance centripetally starting at the mother cell wall and extending into the constricting plasma membrane. Spindle fibers play no direct rôle in the process and a phragmoplast is entirely lacking. More recently McAllister (1931) in an account of the achromatic figure in *Spirogyra setiformis* reports that the new transverse wall between dividing cells develops centripetally through the activity of a phragmoplast which operates essentially as in the higher plants except for its centripetal development. Its centripetal development is undoubtedly the result of the formation of a large vacuole in between the two nuclei, so that the kinkoplasm is pushed centrifugally nearer the wall. In *Spirogyra* cytokinesis is closely related to nuclear division in point of time as in the higher plants.

On the other hand coenocyst formation in *Protosiphon* is suggestive of cytokinesis in certain pollen mother cells as described by Farr (1916, 1918, 1922a, 1922b) and W. K. Farr (1920), in which cell division is accomplished by centripetal furrows which meet at the center of the pollen mother cell at a point equidistant from the four nuclei. The wall substance of the mother cell flows into the furrows so that the bounding membranes of the microspores are formed at least in part from the wall material of the mother cell. Castetter (1925) describes a similar method of cytokinesis in the pollen mother cells of *Melilotus* in which cytokinesis occurs by centripetally developing surface furrows and a series of vacuoles. The mother cell wall, which he claims is made up of callose, flows into the furrows forming the primary walls of the microspores, on the surface of which the microspore protoplasts secrete additional callose. The manner of coenocyst formation in *Protosiphon* is thus essentially similar to cytokinesis in other algae such as *Closterium* and *Cladophora* and to cytokinesis by furrowing in the pollen mother cells of the higher plants. It differs, however, from cytokinesis in *Closterium* and the pollen mother cells in that in these forms, cytokinesis is closely related to the nuclei and their time of division, and

in *Protosiphon* it is thus in this respect more similar to cell division in *Cladophora*.

Comparison of the method of zoosporogenesis in *Protosiphon* with sporogenesis in other algae and fungi reveals many striking similarities. With a view to bringing together some of the data on spore formation in the Thallophyta I have summarized in tables 1 and 2 the names of the species, types of cytokinesis and the names of the investigators. The data on the Ascomycetes were omitted in view of the rather uniform occurrence of free-cell formation in the ascus. Examination of table 1 shows the preponderance of evidence that the prevailing method of spore formation in the coenocytic fruiting bodies of Myxomycetes, Chytridiales, Zygomycetes and Saprolegniales is that of progressive cleavage by furrows, vacuoles or both. In view of the occurrence of alternate contraction and swelling of the cleavage segments in some organisms it is possible that this phenomenon is rather widespread, and that the accounts of simultaneous cleavage in certain species of *Synchytrium* and *Saprolegnia* may be explained by the rapidity with which the earlier stages of cleavage take place, and the corresponding readiness with which they may be overlooked.

From the data on the Chlorophyceae shown in table 2 one can distinguish several categories: the first class includes forms in which the cells are uninucleate throughout the life cycle and remain in that condition up to the time of reproduction. Zoospore and daughter colony formation in these forms is accomplished by a series of nuclear divisions and endogenous cell bipartitions so that the number of cells ultimately produced is a multiple of two. To this group belong such forms as *Chlorogonium*, *Chlamydomonas*, *Gonium* and *Eudorina* and probably all the Volvocales. A similar condition obtains in the Ulotrichales such as *Ulothrix*, *Stigeoclonium*, *Ulva* and *Monostroma*. The second category embraces those genera in which the cell is multinucleate either throughout the life cycle or during the reproductive stage. In these forms zoospore formation is accomplished by progressive cleavage into an indefinite number of segments which develop into the spores. Among such forms should be included *Characium*, *Chlorococcum*, *Hydrodictyon*, *Cladophora* and *Protosiphon*, and probably all the Siphonocladales and Siphonales. As West (1916) considers the coenocytic habit to have arisen secondarily from the more primitive uninucleate condition, it may not be illogical to consider bipartition as the earliest method of cell division. The prevailing method of spore formation in large multinucleate sporangia is by progressive cleavage by furrows or vacuoles.

The homologies of the protospore of such forms as *Synchytrium decipiens* are valuable at least in suggesting possible analogies among certain

TABLE 1
Sporogenesis in certain Thallophyta: Fungi

ORGANISM	BIPARTITION	PROGRESSIVE CLEAVAGE	"SIMULTANEOUS CLEAVAGE"	AUTHORITY	DATE
MYXOMYCETES					
<i>Trichia</i>			" (?)	Strasburger	1884
<i>Fuligo</i>		"		Harper	1900
<i>Ceratiomyxa</i>		"		Olive	1907
<i>Didymium</i>		"		Harper	1914
<i>Physarella</i>		"		Bisby	1914
<i>Stemonitis</i>		"		Bisby	1914
<i>Lycogala</i>		"		Vonwiller	1919
<i>Physarum</i>		"		Howard	1931
CHYTRIDIALES					
<i>Polyphagus</i>		"		Wager	1913
<i>Olpidium</i>			"	Kusano	1912
<i>Olpidiopsis</i>			"	Barrett	1912
SYNCHYTRIUM					
<i>S. Taraxaci</i>			"	Dangeard	1899
<i>S. Taraxaci</i>		"		Harper	1899
<i>S. decipiens</i>		"		Harper	1899
<i>S. Puerariae</i>		"	"	Kusano	1909
<i>S. endobioticum</i>			"	Percival	1910
<i>S. endobioticum</i>			"	Curtis	1921
<i>S. fulgens</i>			"	Kusano	1930
ZYGOMYCETES					
<i>Pilobolus</i>		"		Harper	1899
<i>Sporodinia</i>		"		Harper	1899
<i>Rhizopus</i>		"		Swingle	1903
<i>Phycomyces</i>		"		Swingle	1903
<i>Pilobolus</i>		"		Schwarze	1922
<i>Sporodinia</i>		"		Schwarze	1922
<i>Rhizopus</i>		"		Schwarze	1922
<i>Mucor</i> (2 sp.)		"		Schwarze	1922
<i>Circinella</i>		"		Schwarze	1922
OOMYCETES					
<i>Saprolegnia</i>			" (?)	Rothert	1892
<i>Saprolegnia</i>		"		Schwarze	1922
<i>Achlya</i>		"		Schwarze	1922
<i>Plasmodiopsis</i>			" (?)	Gregory	1912
<i>Plasmodiopsis</i>		" (z)		Nishimura	1926
<i>Phytophthora</i>			" (?)	Ward	1887

of the organisms listed in the table. As Harper (1899) has pointed out, the protospore of *Synchytrium decipiens* represents the culmination of the cleavage process, and the further nuclear and cell division which follow belong to the category of embryonic growth. The homologue of the *Syn-*

TABLE 2
Sporogenesis in certain Thallophyta: Chlorophyceae

ORGANISM	BIPARTITION	PROGRESSIVE CLEAVAGE	"SIMULTANEOUS CLEAVAGE"	AUTHORITY	DATE
<i>Chlamydomonas</i>	" (z)			Kater	1929
<i>Chlorogonium</i>	" (z)			Hartmann	1919
<i>Gonium</i>	" (d.c.)			Hartmann	1924
<i>Eudorina</i>	" (d.c.)			Hartmann	1924
<i>Volvox</i>	" (d.c.)			Harper	1918a
<i>Chlorococcum</i>					
<i>C. infusionum</i>			" (z)	Famintzin	1871
<i>C. infusionum</i>	" (z)			Artari	1892
<i>C. infusionum</i>		" (z)		Bold	1931
<i>C. humicola</i>	" (z)		" (a)	Bristol	1919
<i>Chlorochytrium</i>					
<i>C. Lemnae</i>		" (z)		Cohn	1875
<i>C. Lemnae</i>	" (z)			Klebs	1881
<i>C. bienne</i>	" (z)			Bristol	1920
<i>C. paradoxum</i>	" (z)			Bristol	1920
<i>C. grande</i>	" (z)		" (a)	Bristol	1917
<i>Pediastrum</i>		" (z)		Smith	1916b
<i>Pediastrum</i>	" (z)			Harper	1918b
<i>Characium</i>		" (z)		Smith	1916a
<i>Tetradron</i>		" (a)		Smith	1918
<i>Scenedesmus</i>	" (d.c.)			Smith	1914
<i>Sorastrum</i>			" (z)	Geitler	1924
<i>Hydrodictyon</i>		" (z)		Timberlake	1902
<i>Hydrodictyon</i>		" (z)		Harper	1908
<i>Ulothrix</i>	" (z)			Gross	1930
<i>Ulothrix</i>	" (z)			Cholnoky	1932
<i>Stigeoclonium</i>	" (z)			Cholnoky	1928
<i>Monostroma</i>	" (z)			Carter	1926
<i>Ulva</i>	" (z)			Carter	1926
<i>Cladophora</i>		" (z)		Czempyrek	1930
<i>Sphaeroplea</i>		" (o)		Klebahn	1899
<i>Codium</i>			" (g)?	Williams	1925
<i>Derbesia</i>		" (z)		Davis	1908
<i>Rhodochytrium</i>		"	"	Griggs	1912

Letters in parentheses denote type of spore formed: (a)=aplanospore, (d.c.)=daughter colony, (g)=gametes, (o)=oospores, (z)=zoospores.

chytrium protospore in the developing zoosporangium of *Protosiphon*, is the uninucleate segment which is delimited at the completion of cleavage. It is homologous not only in method of formation but also in its subsequent development into swarmspores. The essential point of divergence is that in *Synchytrium decipiens* the multinucleate stage of the protospore, the spore which results from its embryonic development, is not immediately subdivided into swarmspores as is the case in *Protosiphon*; swarmspore formation in *Synchytrium* may be regarded as a germination stage as in certain Oomycetes. The formation of a clear area in the cytoplasm of the protospores between the nuclei before the final bipartitions is highly suggestive of what occurs in the final cleavage stages in *Fuligo*.

Harper has already pointed out the abbreviation of the cleavage process in *S. Taraxaci* as compared with *S. decipiens*, and in *Sporodinia* as compared with *Pilobolus*. The same relation holds in zoospore formation in the thalli as compared with the mature coenocysts of *Protosiphon* and the thalli of *Chlorococcum infusionum*, for although the process is essentially similar in all three, it is more abbreviated in the smaller coenocysts and *Chlorococcum* cells, in which because of their smaller size, the primary cleavage furrows may directly delimit uninucleate protospores.

In none of the other Chlorophyceae so far reported are there any stages homologous with the embryonic development of the protospore of *Protosiphon*. Timberlake describes the direct transformation of the uninucleate segment or protospore of *Hydrodictyon* into the swarmspore. This is true of the majority of forms reported. In view of Smith's (1930a) contention that *Halicystis* and *Protosiphon* are closely related it will be especially significant to compare the progressive cleavage in *Halicystis*, which he has described in a preliminary account, with the same process in *Protosiphon*, when figures of the former genus are available.

The mechanical principles involved and their operation in the process of cleavage are still uncertain. The similarity to segmentation of drying colloidal substances suggested to Harper that cleavage in the fungi which he studied might be essentially a drying-out process in which the nuclei function as centers of water retention. Cleavage in *Protosiphon*, *Hydrodictyon*³ and the water molds, however, cannot be due to drying out in the same sense, since it occurs in these forms only when they are submerged. There can be no doubt from the data on the large number of forms investigated that changes from higher to lower water content of the spore plasm take place during zoospore formation. Loss of water in submerged forms, however, is plainly initiated and controlled throughout by the cell.

³ See Harper (1908) for a discussion of cleavage in the living cells.

The hypothesis of water loss by drying as a possible explanation of the phenomenon of cleavage in submerged sporangia can possibly be applied to these forms if one emphasizes that this "drying" is autonomous on the part of the protoplasm.

It is apparent in the literature on sporogenesis outlined above, that some confusion exists as to the usage and meaning of the various terms describing types of cytokinesis. I have attempted in the following discussion, to clarify the different types of cell division described in the literature as far as I have been able to understand them.

According to Strasburger (1880) Schleiden first employed the term "free-cell formation" to designate the origin of cells within a protoplasmic mass, which process he considered to take place through the formation of granules in the homogeneous plasm (cytoblastema), about which other granular material collected, thus forming transparent vesicles, (cells) or "cytoblasts." The term was later extended by Hofmeister (1867) to include other cases of cell formation. First, the formation of the spores of the phanerogams, gymnosperms, vascular cryptogams and mosses; second, the formation of endosperm in the phanerogams, and the gametophyte from the megaspores of certain lycopods; and finally the development of the spores of lichens and ascomycetes, and those fungi which form their reproductive cells free within the mother cell. Strasburger (1880) in his general discussion of cell division and formation, concludes that the category of free-cell formation includes not only such cases as endosperm formation in the higher plants, but also such as the formation of the swarmspore in *Oedogonium* ("Vollzellbildung") and also the formation of a number of spores in a sporangium ("Vielzellbildung"). Probably on the basis of these conceptions, West (1916), Cohn (1875) and others refer to the formation of algal zoospores by "free-cell formation." Since 1880 however the term has come to be used in a rather limited sense, as referring especially to spore formation in the ascus, and Harper (1899) proposed to restrict its usage to the type of division found in the ascus. At the same time he pointed out that the process is quite different both from endosperm formation in the flowering plants and from the progressive cleavage by constriction which occurs in coenocytic sporangia; for in the ascus, a cell is delimited *within* the *protoplasm* of its mother, and a residual *epiplasm* remains. It is now generally agreed that the intersporal slime in coenocytic sporangia bears no relation to the *protoplasmic* residue in the ascus. In view of these confusing usages, and the fact, as pointed out above, that most cases of spore formation in algae and fungi occur by surface constrictions (bipartition and multipartition or progressive cleavage), it would perhaps make for greater clarity to retain the term "free-cell for-

mation" for those cases in which a cell is cut out from the protoplasm of a mother cell in such a way that residual protoplasm (epiplasm) remains. This category would then include spore formation in the ascus (which is accomplished through the agency of knoplastic fibers) as well as cell formation in the pro-embryo of *Ephedra* (Strasburger, 1880).

The term progressive cleavage was first applied by Harper (1899) to the process of segmentation of coenocytic fungus sporanges, in which delimitation of the spores is a progressive process, always progressive as far as the formation and deepening of the furrows is concerned, and often but not always progressive in that at first larger, and subsequently smaller masses of protoplasm are delimited.

Strasburger (1875) was probably the first to call spore formation simultaneous as Schwarze has pointed out, and the term has been applied to sporogenesis in a great series of forms by a number of investigators; as noted above, in view of the alternate swellings and contractions in sporangia and the rapidity with which sporogenesis is accomplished, it is reasonable to suppose on the basis of available data that there is no convincing evidence for the occurrence of a "simultaneous cleavage" process. If it could be demonstrated for some organism, that clefts are formed simultaneously throughout their entire extent such a process would have to be made a separate category. In my opinion no one has demonstrated it convincingly, and all cases of so-called "simultaneous cleavage" upon re-investigation will undoubtedly fall into either the category of progressive cleavage or successive bipartition.

I have summarized these possible categories of cell as contrasted with nuclear division in the following table. As is the case with all such attempts, future investigation may show such a grouping false and misleading in many particulars.

Categories of cytokinesis as contrasted with karyokinesis

- I. Segmentation by surface furrows or apparent constrictions including furrows originating at the surface of vacuoles.
 - A. Bipartition: formation of two cells from one; cells not necessarily equal in size.
 1. Bipartition more or less directly following nuclear division.
 - a. division of flagellates.
 - b. holoblastic cleavage in homolecithal animal eggs.
 - c. cell division in *Closterium*.
 - d. zoospore formation in *Ulothrix*.
 - e. conidia formation in the mildews.
 2. Bipartition not directly related in time and sequence to nuclear division.
 - a. formation of the coenogametes in *Sporodinia*.
 - b. zoospore formation in *Pediastrum*.
 - c. cell division in *Cladophora*.

B. Multipartition, or progressive cleavage, including quadri-partition in certain pollen mother cells;⁴ segmentation process relatively independent of nuclear division.

1. Partition by surface furrows only.

- a. spore formation in the sporangia of many coenocytes such as *Synchytrium*, *Protosiphon*, etc.
- b. cleavage in centrolecithal animal eggs.
- c. segmentation of certain pollen mother cells (see Farr).
- d. coenocyst formation in *Protosiphon*.

2. Partition by surface furrows and vacuolar furrows.

- a. columella formation in *Pilobolus* and *Sporodinia*.
- b. spore formation in *Rhizopus* and *Phycomyces*.
- c. segmentation of the pollen mother cells of *Melilotus* (see Castetter).
- d. cell formation in the plasmodium of human embryonic epithelium. (see Sharp, 1926, p. 15.)

II. Segmentation by cell-plate formation.

A. Cell-plate formation closely associated with or involving the achromatic figure or kinoplasm. (Cytokinesis by phragmoplast.)⁶

1. Path of cell plate a flat plane.

a. Path centrifugal.

Bryophytes, Pteridophytes, Spermatophytes—all vegetative cells; endosperm formation in the angiosperms (so far as known).

b. Path centripetal.

Spirogyra setiformis. (McAllister.)

2. Path of cell-plate curved or circular.

a. wall formation in the generative cells of *Abies* and *Picea* by curved phragmoplast⁶ and cell-plate. (Hutchinson, 1914, 1915.)

b. wall formation in the antheridium of certain ferns. (Strasburger, 1880.)

B. Cell-plate formation apparently not involving directly the achromatic figure or kinoplasm.

1. cell division in *Cladophora*.

2. cell division in *Stypocaulon*. (Swingle, 1897.)

3. segmentation of the oogonium in *Fucus*. (Farmer and Williams, 1898.)

III. Free-cell formation: cells arising within the protoplasm of a mother cell, leaving residual protoplasm: epiplasm in the ascus, periplasm in the oogonium of the Peronosporales.

A. Free-cell formation clearly involving the activity of kinoplasmic fibers.

1. spore formation in the ascus.

2. cell formation in the pre-embryo of *Ephedra*.

⁴ In preparations showing the divisions of the pollen mother cells in certain *Viola* hybrids, the author has observed the formation of as many as twelve uninucleate microspores by furrowing, which suggests a rather close connection between the process in pollen mother cells and other cases of furrowing by surface constriction.

⁶ As pointed out to the author by Professor F. McAllister, the term *phragmoplast* was probably first used by Errera (1888).

⁶ The activity of curved and circular phragmoplasts suggests in some degree, the process of free-cell formation as it occurs in the ascus.

- B. Free-cell formation not directly involving the activity of kinoplasmic fibers (so far as known).
1. cell-wall formation in the angiosperm zygote.
 2. formation of the female gamete in the Peronosporales.

I have listed under these possible categories, cases well known from the literature as far as I have been able to interpret them. A glance at the examples mentioned above, is sufficient to show that in all cases, the active agent of cytokinesis is either the constricting surface membrane, or kinoplasmic fibers. In view of the evidence for the close relation between kinoplasmic fibers and surface membranes, on the basis of future work it may be possible to clarify the relations between the categories still further.

The periodicity of swarmspore liberation so often reported in aquatic organisms like *Hydrodictyon*, *Pediastrum* and *Chlorococcum* is entirely absent from the terrestrial *Protosiphon* as far as my observations go. The stimulus which causes zoospore formation and escape in this organism is water, and submersion of mature thalli in water always results in liberation of motile cells without relation to time of day or light intensity.

The structure of the zoospore is similar to that of most of the Chlorophyceae so far studied cytologically. Although I have been unable conclusively to trace the origin of the blepharoplast from the nucleus, it is very certain that it is not a localized swelling of the plasma membrane as Strasburger described in the swarmspore of *Cladophora*. It always stains intensely with safranin, while the plasma membrane shows avidity for gentian violet; the presence of a rhizoplast is further evidence of its relation to the nucleus.

Should the reduction division be found to take place in the first division of the germinating zygospore, as is suggested by some cytological evidence at hand, *Protosiphon* would fall into the same category with the other haplobiontic Chlorophyceae such as *Coleochaete*. While gametes from the same plant do not usually conjugate, the occasional presence of zygospores within the old wall of a single plant would suggest that heterothallism is not so firmly established in *Protosiphon* as it has been reported to be in other Chlorophyceae such as *Cladophora*, *Enteromorpha*, *Chaetomorpha* and *Ulothrix*.

In studying ontogeny, structure and phylogeny of *Protosiphon* in relation to other members of the Chlorophyceae two views are to be considered, as Smith (1930a) has pointed out. First, *Protosiphon* may be looked upon as having developed from an organism of the *Chlorococcum*, *Chlorochytrium* type, in which the multinucleate condition became fixed, and the stimulus of a terrestrial habitat led to the formation of a subterranean rhizoid. The isogamous reproduction of *Protosiphon* is similar

to that in these genera. According to the second view, the coenocytic character of the thallus, and its differentiation into a rhizoidal and expanded aerial portion, are highly suggestive of conditions found among the Siphonales. On this basis *Protosiphon* could be included among those Siphonales with simpler vegetative structure and more primitive reproduction. It appears that the second view is more logical for several reasons. While the tendency to the coenocytic habit appears in certain forms of the Chlorococcales it has become the general rule in *Protosiphon*. The coenocytic habit according to most systems of classification is the most fundamental requisite for admission into the Siphonalian alliance.

The objection to including *Protosiphon* among the Siphonales because of its somewhat specialized habitat and form does not carry weight, in view of the fact that organs of anchorage appear again and again not only in terrestrial forms but in many members of the submerged Siphonales and even in such a form as *Spirogyra*, under certain conditions. On the contrary the somewhat special organization of the *Protosiphon* thallus is more in line with that of the Siphonales in general, since in this group the organization of the thallus reaches the highest state of development in the Chlorophyceae. Although no cases of isogamous reproduction have been reported among the Siphonales as far as I am aware, our present system of classification of Chlorophyceae is based largely on characters of the thallus, and there are many examples of the fact that degree of specialization in reproduction is not always correlated with a corresponding degree of thallus development. For these reasons isogamous reproduction in *Protosiphon* should be no serious obstacle to placing it among the Siphonales. Smith (1930 a) has noted that morphologically *Protosiphon* is the fresh water equivalent of the marine *Halicystis* except that the latter is considerably larger and has anisogamous gametes. For these reasons it seems more natural to consider the family Protosiphonaceae with the genera *Protosiphon* and *Halicystis* among the simpler Siphonales as West (1916) and Setchell and Gardner (1920) have done. One further point is significant. Among the Heterokontae if we accept West and Fritsch's (1927) and Pascher's (1925) group Heterosiphonales as exemplified by *Botrydium* alone, as an order parallel with the Siphonales of the Isokontae, it is at the very least highly inconsistent to relegate *Protosiphon* to the Chlorococcales.

SUMMARY

1. *Protosiphon botryoides* Klebs is a cosmopolitan species occurring on damp soil together with *Botrydium*. At the mature stage of vegetative development the thallus consists of a single cell with an aerial, expanded, bulb-like portion and an unbranched subterranean rhizoid. The plant is

coenocytic throughout its life cycle, returning to the uninucleate condition only during reproduction.

2. There is a large central vacuole and there is no evidence for the presence of distinct and localized chromatophores in the cells of *Protosiphon* such as are found in *Nitella*, *Botrydium* and other forms. On the contrary the chlorophyll completely pervades the cytoplasm, as evidenced by the random position of pyrenoids throughout the primordial utricle. Transition from the chlorophyll-bearing to colorless cytoplasm in the rhizoidal portion is gradual rather than abrupt.

3. The relation of the pyrenoid to starch formation is identical with that described by Timberlake in *Hydrodictyon*. Proteinaceous segments split off from the pyrenoid, are pushed out into the cytoplasm and become transformed into starch grains, staining successively brilliant red, reddish purple, and finally blue with the Fleming triple stain.

4. Reproduction is accomplished by separation of lobes and branches of thalli from young parent plants by septa; by formation of zoospores from thalli and coenocysts, which may function as gametes, fusing in pairs and forming thick-walled zygospores. The zygospore germinates after a period of dormancy into a new thallus. Zoospores also develop without fusion into new thalli. Zoospores which are not liberated from the parent cell develop walls within it and by their further growth into new thalli, rupture the mother thallus wall. Segmentation of the thallus protoplast into a number of multinucleate coenocysts occurs in periods of drought, and after continued exposure to sunlight these cysts develop a red pigment. In a moderately moist substratum the cysts can develop directly into the thallus, or when submerged in water, form zoospores. (Text fig. 1 illustrates the life history of *Protosiphon*.)

5. Coenocysts arise by the centripetal growth of furrows originating at the plasma membrane, and progressing through the cytoplasm. Wall material, continuous with the wall of the thallus, is secreted into the furrows by the protoplasm. The process is in some respects similar to that of cell division in *Closterium* and *Cladophora* and to cytokinesis in the pollen mother cells of certain higher plants.

6. Zoospore formation in thalli and cysts takes place by a process of progressive cleavage. The protoplast shrinks from the cell wall by extrusion of water from the plasma membrane and central vacuole. Furrows form at the surface of the plasma and tonoplast and cut progressively deeper into the protoplasm thus delimiting first multinucleate, and finally uninucleate segments or protospores. By further nuclear and cell division these segments give rise to the zoospores. The protospore of *Protosiphon* is similar to that of *Synchytrium decipiens*, *Pilobolus* and *Hydrodictyon*.

It differs from that in the last named organism only in undergoing embryonic development antecedent to forming the zoospores. The autonomous nature of dehydration of the protoplast during cleavage of submerged is stressed.

7. Zoospores and functional gametes of *Protosiphon* are bi-flagellate, naked protoplasts with a single stigma, two contractile vacuoles and with or without pyrenoids. The presence or absence of the pyrenoid is correlated with its disappearance or fragmentation during zoosporogenesis. The nucleus is anterior and connected to the blepharoplast by a single rhizoplast. In conjugation two gametes establish contact in the region of the blepharoplast and fusion proceeds from the anterior toward the posterior region. Syngamy occurs from three to four hours after the initiation of plasmogamy. As zoospores and zygospores come to rest the flagella are withdrawn into the cell. Gametes from the same thallus or coenocyst as a rule are incompatible, although occasionally zygospores may be found within a single mother cell.

8. Nuclear division is simultaneous throughout the thallus, but not completely synchronous, nuclei at the apex or base of the cell usually being more advanced. The structure of the nucleus is similar to that of the nuclei of the higher plants in that nucleoli, chromatin and nuclear membranes are present. The nucleole apparently plays no part in the formation of the chromosomes, disappears during the prophase, and is re-organized in the daughter nuclei.

9. *Protosiphon* along with *Halicystis* should be placed among the simpler Siphonales as West (1916) and Setchell and Gardner (1920) have done, rather than retained among the Chlorococcales.

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Explanation of plates 10-19

All figures were drawn with the aid of a camera lucida, using a Leitz 1/16 oil immersion objective or a Bausch and Lomb 1.8 mm Fluorite oil immersion objective with various compensating oculars. The approximate magnification is given in the descriptions of the figures. Plates 13 and 14 are slightly reduced.

Fig. 1. Longitudinal section of an almost mature thallus. $\times 760$.

Figs. 2, 3. Median longitudinal sections of rhizoids of young thalli. $\times 1200$.

Fig. 4. Immature thallus from densely inoculated culture. $\times 1540$.

Fig. 5. Cross section of thallus through expanded portion; tonoplast separated from primordial utricle in certain regions. $\times 760$.

Fig. 5a. Portion of preceding thallus enlarged. $\times 2400$.

Figs. 6-10. Starch formation from pyrenoids. $\times 2400$.

Figs. 11, 12. Condition of resting nuclei. $\times 2400$.

Figs. 13, 14. Prophases of nuclear division. $\times 2400$.

Figs. 15-17. Anaphase, equatorial plate, and telophase stages. $\times 2400$.

Fig. 18. Longitudinal section of an immature thallus illustrating progressive synchronism of nuclear division. $\times 1540$.

Figs. 19-23. Stages in the development of the thallus from the zoospore stage. $\times 1540$.

Fig. 24. Dormant zygote from same preparation as preceding. $\times 1540$.

Figs. 25-27. Sections of encysting thalli at different stages. $\times 1540$.

Fig. 28. Encystment completed; thallus completely divided into mature coenocysts. $\times 760$.

Fig. 28a. Median longitudinal section of a rhizoid after encystment. $\times 1540$.

Fig. 29. Cross section of mature thallus after immersion in water, illustrating progressive cleavage in zoosporogenesis; pyrenoid fragments evident in cytoplasm; nuclei in interphase condition. $\times 1540$.

Fig. 30. Median longitudinal section of an immature thallus in the protospore stage of zoosporogenesis. Note remnant of the central vacuole. $\times 1540$.

Fig. 31. Cross section of thallus illustrating primary segmentation by furrows into multinucleate blocks, some of which are undergoing further furrowing.

Fig. 32. Oblique section of thallus showing early stages of progressive cleavage and the vacuolar remnant at one side of the protoplast. $\times 1540$.

Fig. 33. Portion of a section of a thallus at the uninucleate or protospore stage at the completion of cleavage. $\times 1540$.

Fig. 34. Nuclear division in the protospores illustrating almost complete synchrony. $\times 1540$.

Fig. 35. Bipartition of binucleate protospores after nuclear division. $\times 1540$.

Fig. 36. Dividing protospores more highly magnified showing the clear zone in the equatorial region. $\times 2400$.

Fig. 37. Partial section of thallus shortly after motility of zoospores has been initiated. $\times 1540$.

Fig. 38. Immature coenocyst soon after formation with highly vacuolate protoplasm. $\times 1540$.

Figs. 39, 40. Successive stages in the maturation of coenocysts. $\times 1540$.

Fig. 41. Zoosporogenesis in an immature coenocyst. $\times 1540$.

Fig. 42. Partial section of a more mature coenocyst during cleavage. $\times 1540$.

Fig. 43. Cleavage in a small, but mature coenocyst. $\times 1540$.

Fig. 44. Protospore stage in zoosporogenesis of a coenocyst. $\times 1540$.

Fig. 45. Zoospores soon after initiation of motility within the mother thallus, greatly magnified; rhizoplast, blepharoplast and flagella visible. $\times 2400$.

Fig. 46. A single zoospore initial before the development of flagella, illustrating the close association of the blepharoplast with the nucleus.

Fig. 47. Mature and actively swimming zoospores before liberation from the mother thallus. $\times 1540$.

Fig. 48. Division of the protospore nuclei at the conclusion of cleavage in a coenocyst. $\times 1540$.

Fig. 49. Protoplasts formed as a result of bi-partition of the protospores. $\times 1540$.

Fig. 50. Bi-partition after nuclear division in the protospores. $\times 1540$.

Fig. 51. Probable second nuclear division of the protospores. (Compare with Figs. 48 and 49.) $\times 1540$.

Fig. 52. Zoospores at the initiation of motility within the mother coenocyst. $\times 1540$.

Figs. 53–58. Stages of plasmogamy. $\times 2500$.

Figs. 59–61. Stages of syngamy. $\times 2500$.

Fig. 62. Dormant zygote. $\times 2500$.

Figs. 63, 64. Prophases of nuclear division in the germination of the zygote. $\times 2500$.

Fig. 65. Binucleate stage of the germinating zygote. $\times 2400$.

Fig. 66. Tetranucleate stage of the germinating zygote. $\times 2500$.

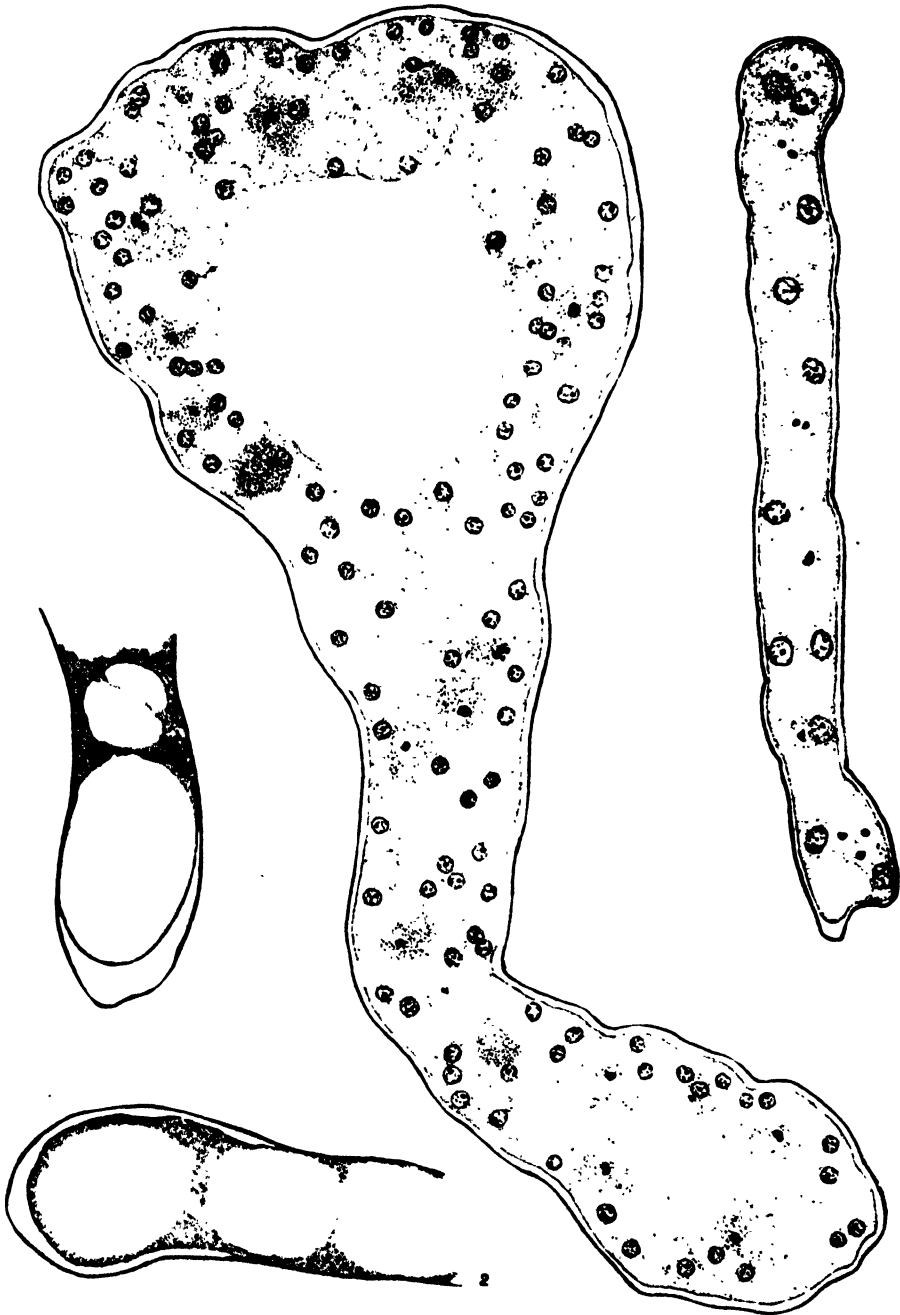
(Figs. 67–75 are from living cells.)

Fig. 67 a–h. Plasmogamy of living gametes in a hanging drop culture. Contractile vacuoles, stigmas and flagella visible. $\times 1540$. i. Portion of the margin of the drop illustrating zoospores and zygotes as they come to rest. $\times 1540$.

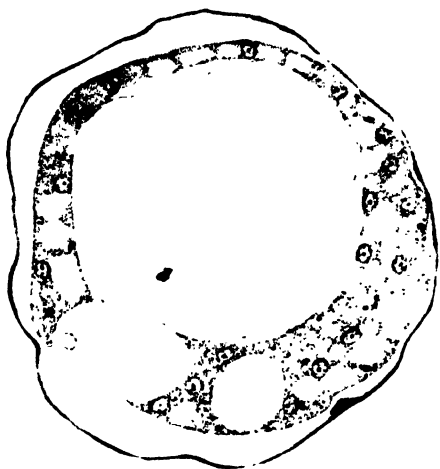
Fig. 68. Variation in size and shape of zoospores. End view illustrated at *a*. $\times 1540$.

Figs. 69–73. Stages of growth of the zoospore into the thallus. 69a. zygote entering dormancy. $\times 1540$.

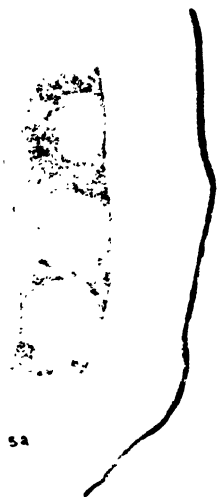
Figs. 74, 75. Branching of young thalli and separation of the branches by partitions. $\times 1540$.



BOLD : PROTOSIPHON



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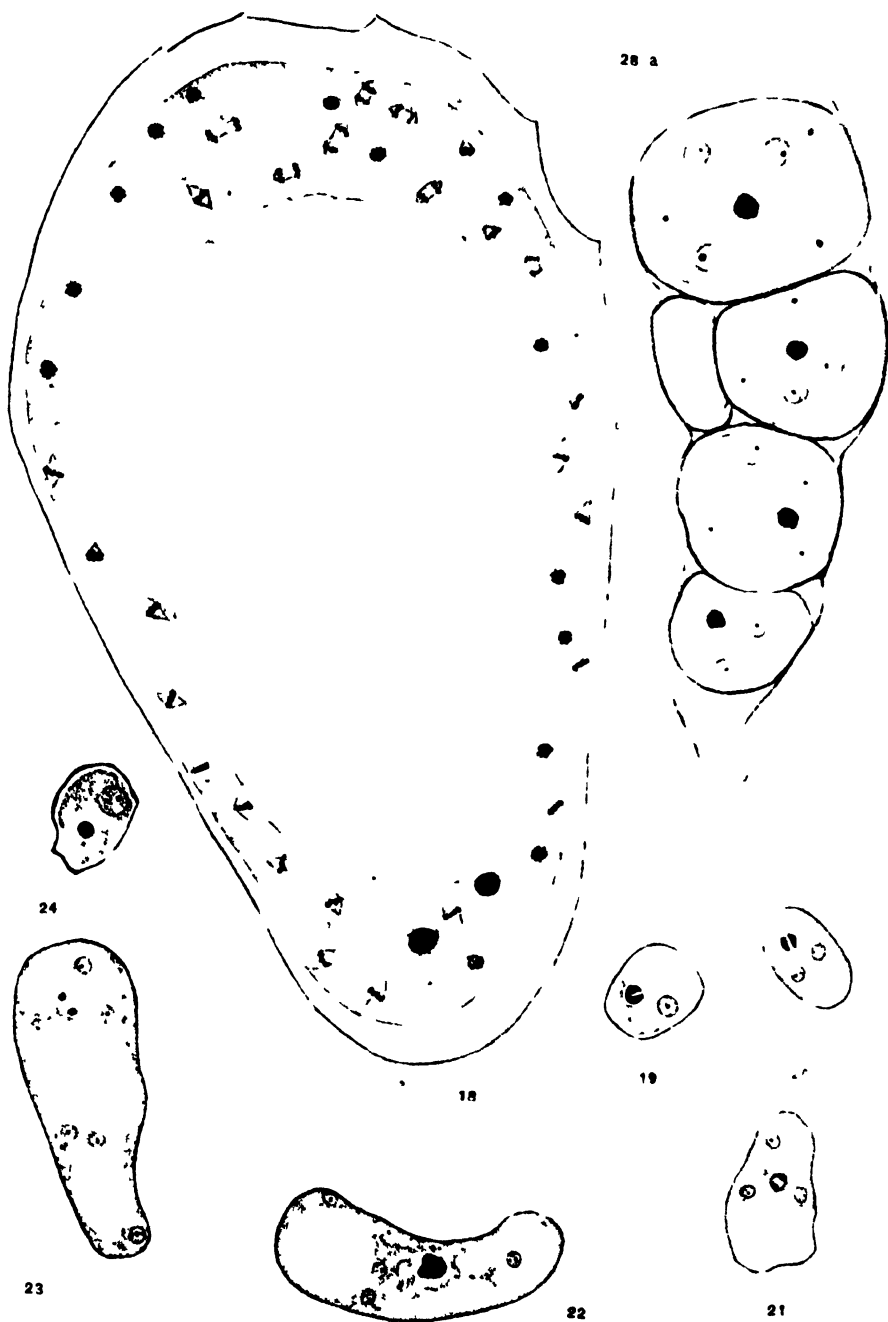
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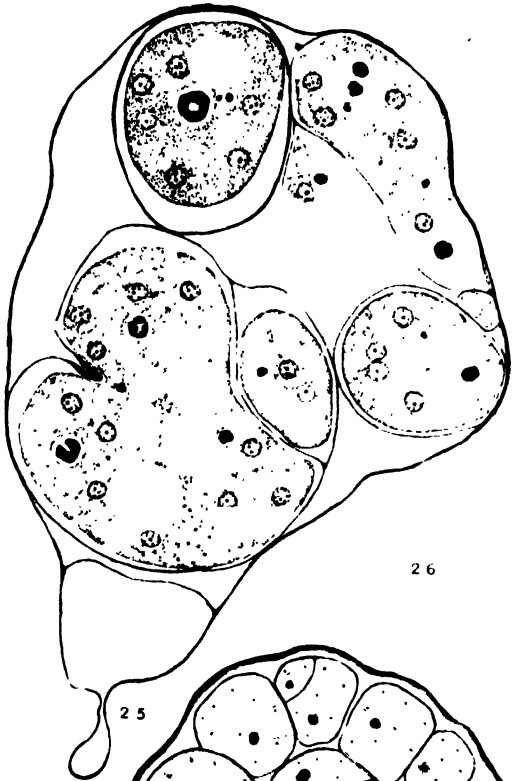
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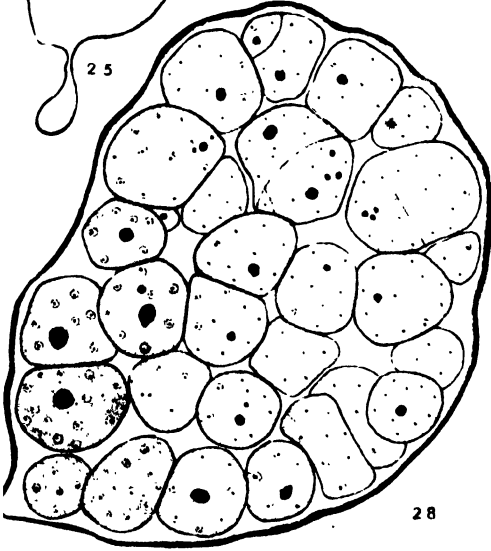
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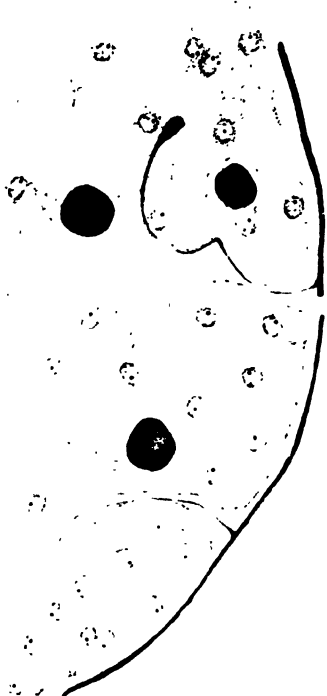
BOLD PROTOSIPHON



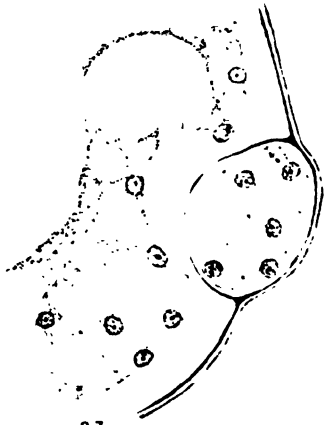
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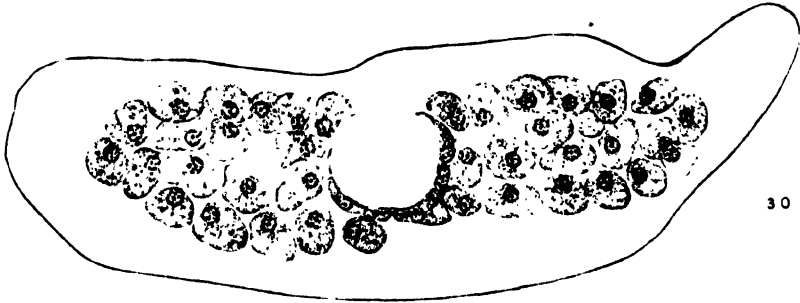
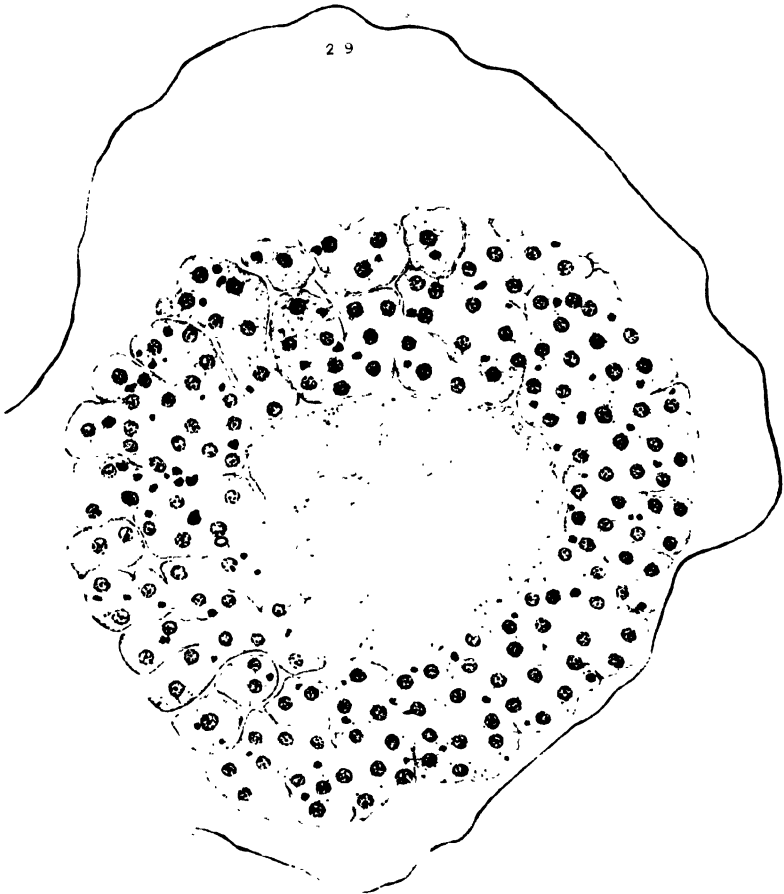
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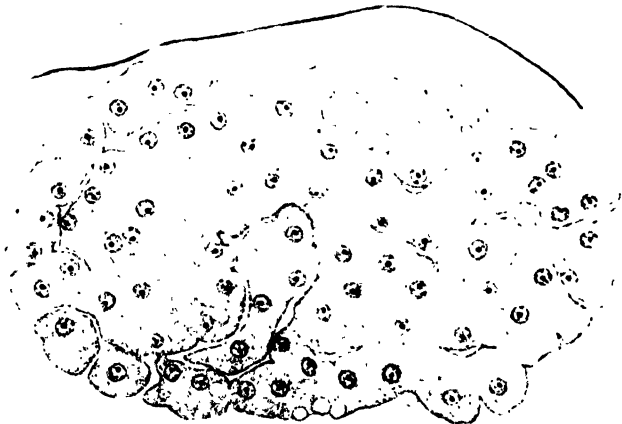
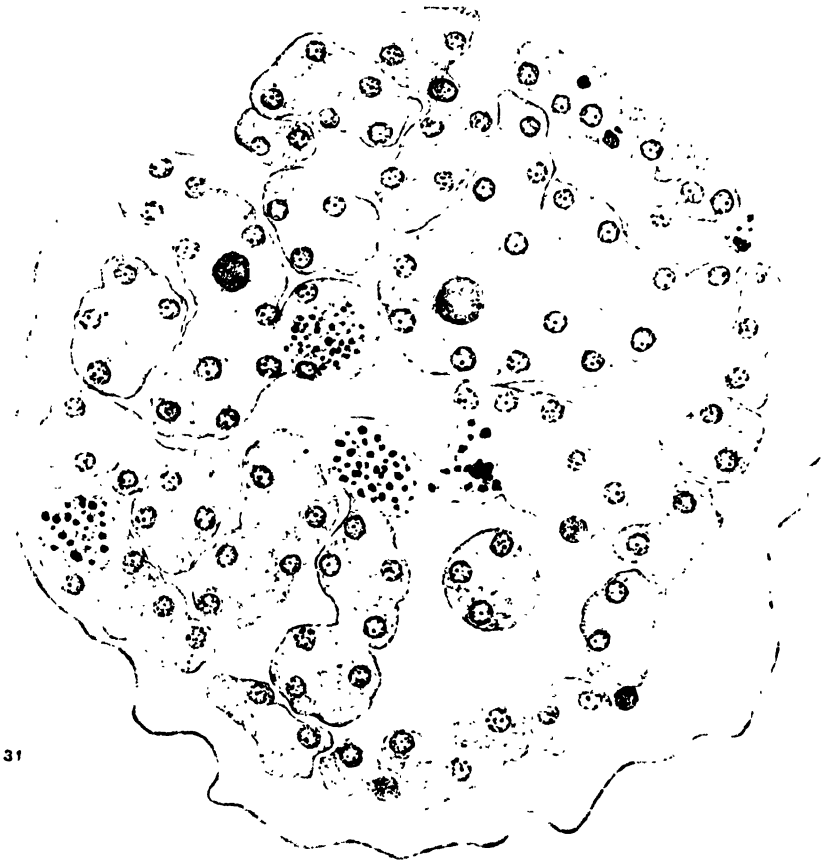


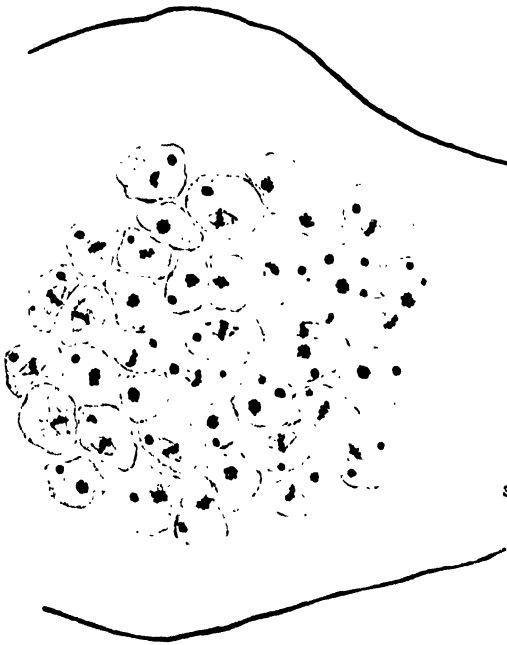
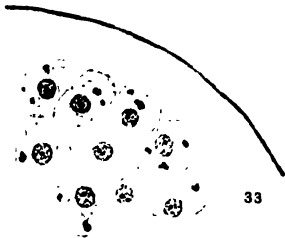
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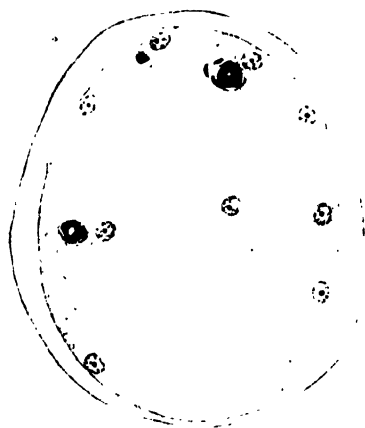


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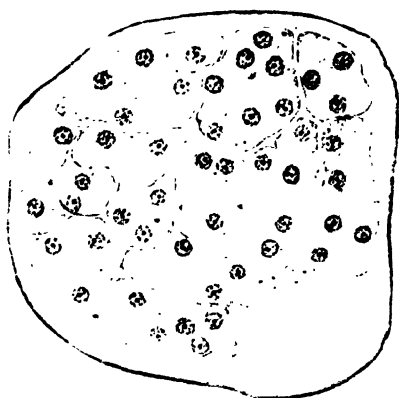




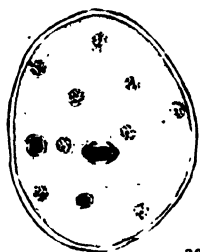




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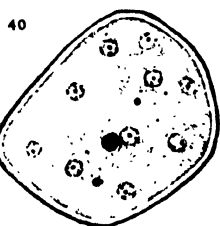
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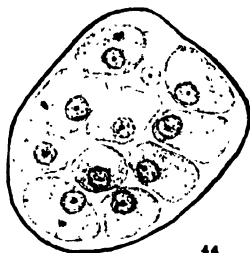
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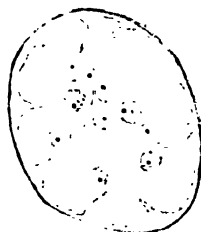
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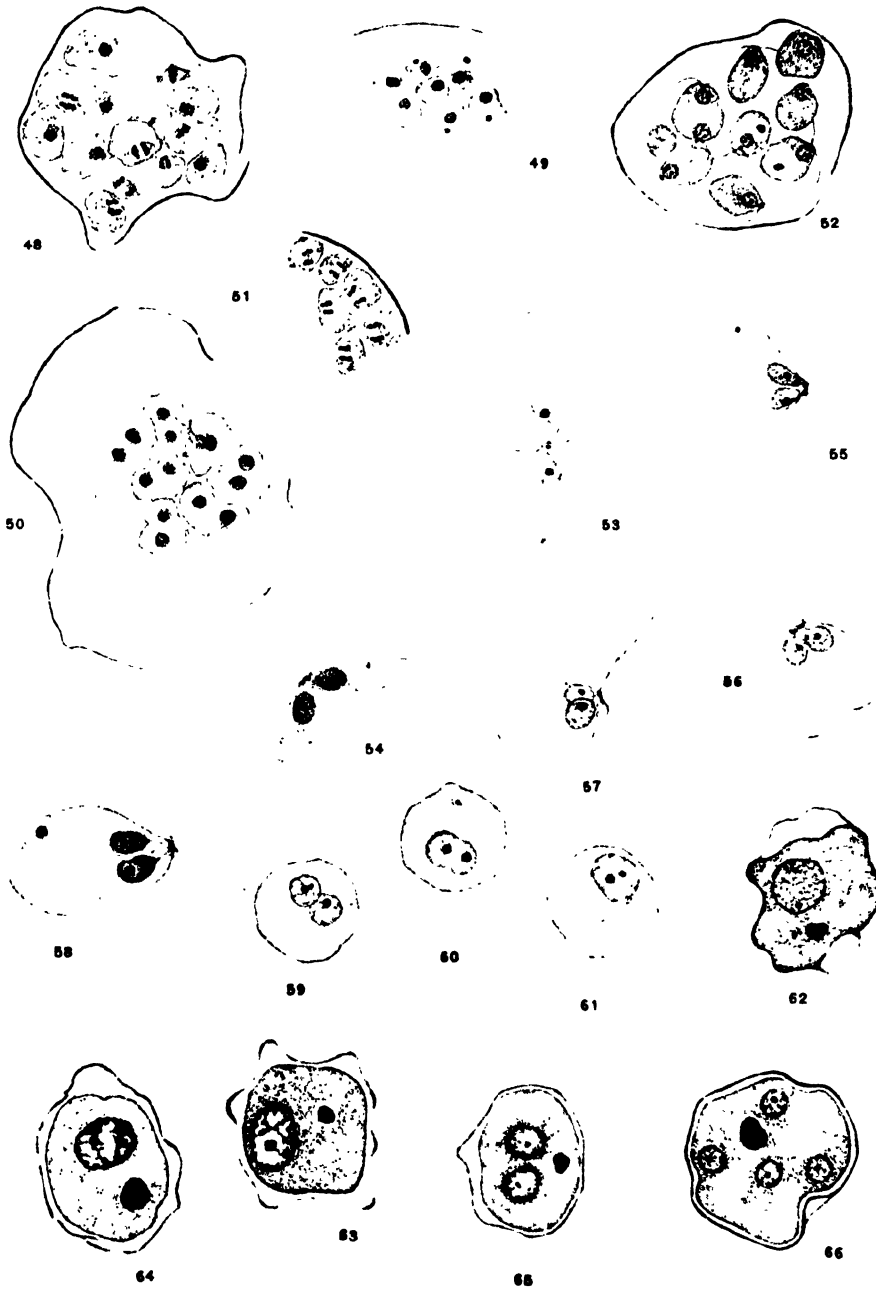
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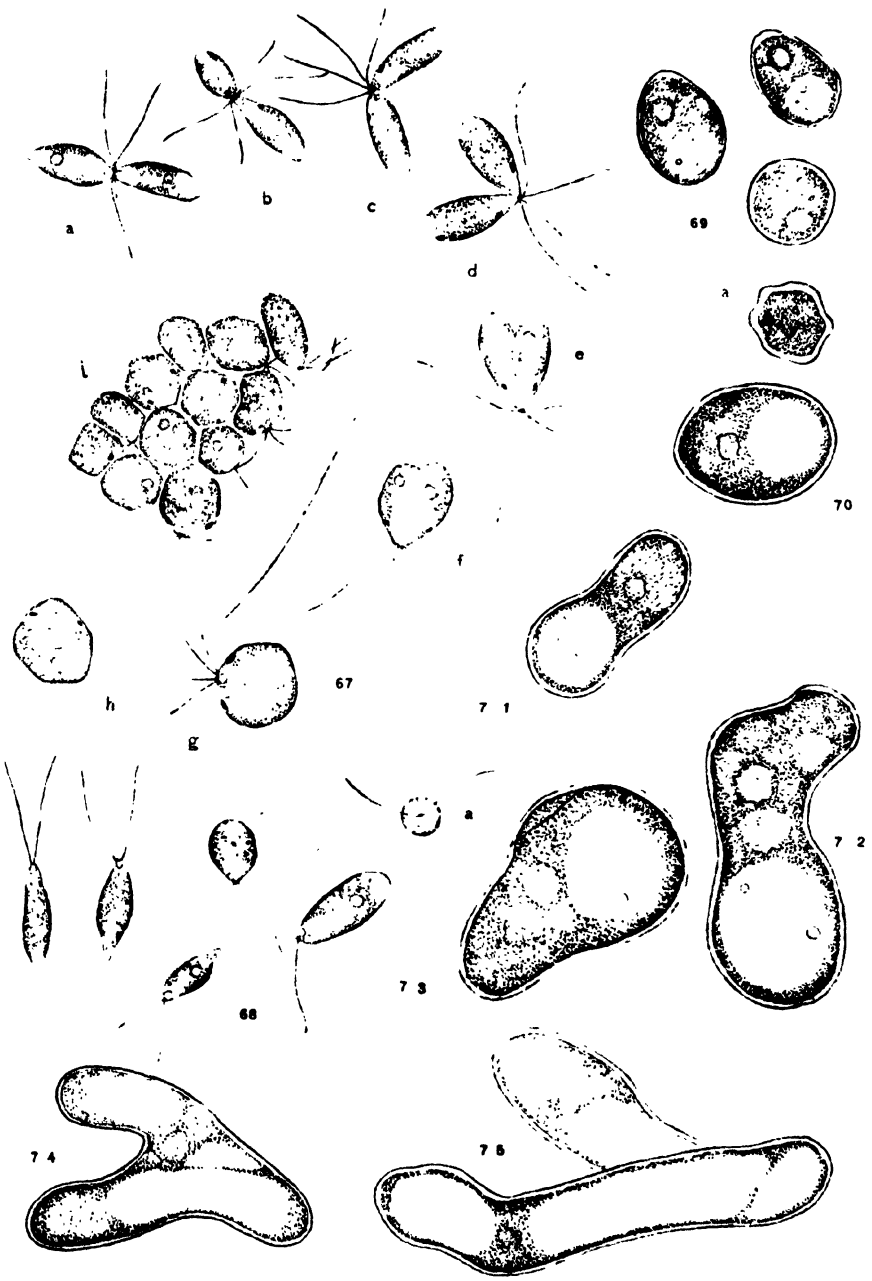


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Plant succession at the borders of a kettle-hole lake

H. W. GRAHAM AND L. K. HENRY

(WITH EIGHT TEXT FIGURES)

During the summer of 1926 while located at a camp at Deep Pond near Wading River, Long Island, the senior author was impressed with the striking zonation of the plants on the shore of the lake. These zones were not the associates commonly found at the borders of lakes representing increasingly drier conditions progressing from the water, for several zones occurred on the dry beach where the edaphic conditions were apparently more or less uniform. Deep Pond is a kettle-hole lake dependent upon the main water table, the surface of the lake being in the plane of the ground water. Consequently, fluctuations in the height of the water table cause variations in the level of the lake. It was learned from local residents that the level of the lake had been falling for several years and was, in 1926, at a very low stage. A study of the vegetation about Deep Pond at that time indicated that the zonal segregation of the shore plants was associated with the annual recessions of the lake during the preceding years.

The results of these observations were discussed with the junior author who was located at Deep Pond during the summers of 1929 and 1931. His investigations in those two years showed that the assumptions made in 1926 were largely correct, namely, that the vegetation on the shore of the lake is an ever-changing community responding to the fluctuations in environment due to the oscillations of the lake level. During periods of rising water there is a denudation of the area submerged caused by drowning and the scouring action of the waves and ice. During this phase of the cycle there is a progression of hydrophytic and aquatic plants from the floor of the lake. During periods of falling water level denuded strips of shore are exposed and there is a progression of mesophytic and xerophytic plants from the pine barrens bordering the lake.

During the winter months of a period of lowering water level, portions of the beach are exposed which cannot be invaded by plants because of the dormant state of the vegetation. Consequently, by the time growth is resumed in the spring a strip of denuded beach has been exposed. Certain moisture-loving plants quickly occupy this strip, the same plants which occupied the adjacent strip exposed the preceding year. This adjacent strip, however, is now occupied predominantly by other plants, more mesophytic in character, which were in the strip exposed two years before. As a consequence, this succession of plants in the denuded shore presents concentric zones about the lake which represent the annual recessions of

the lake level. As the lake recedes certain hydrophytes are left stranded above water. The more tolerant of these may remain for a time in the first shore zone and are sometimes found there with some of the more meso-phytic forms. Similarly, during periods of rising water level, particularly

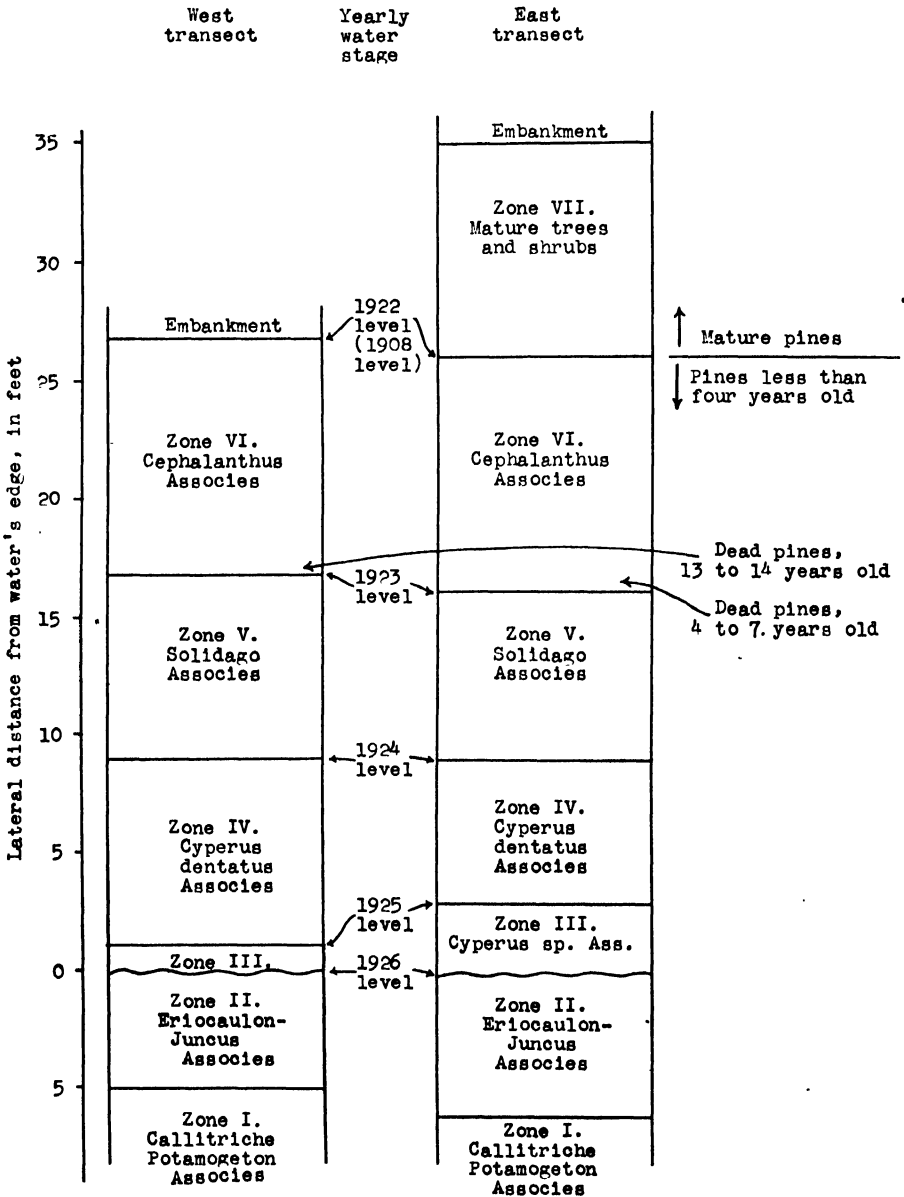


Fig. 1. Vegetation zones at the borders of the lake during the low water stage of 1926.

when the rise is rapid, certain submerged mesophytes may survive for a short time with the invading hydrophytes.

The lake level in 1926 was unusually low and proved to be the lowest of the current recession. When the lake was visited three years later, in 1929, its level had risen considerably, drowning many of the plants which had become established on the exposed beach during the recession ending in 1926. This rise which was observed in 1929 probably reached its maximum late in that year for local reports stated that the lake level was again dropping during 1930. This recession continued to 1931. When the lake was visited in 1931 it was found to have dropped 15 inches since 1929, ex-

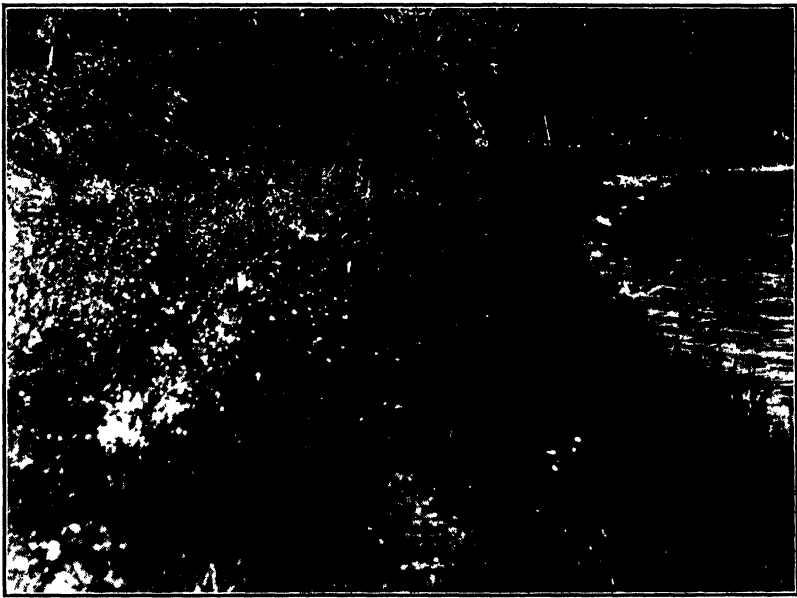


Fig. 2. Vegetation on west shore of lake in 1926 at time of lowest water level of the recession. In 1922 the lake was up to the base of the embankment to the left. Numerals indicate the four shore zones extending from this level to the water's edge. Footpath can be seen in the center of Zone IV.

posing from 12 to 13 feet of beach line. On this exposed beach another plant succession was already taking place. The remains of many of the plants of the previous succession still persisted and were mixed with the plants of the latest succession.

Thus, from these few years' observations it was strikingly demonstrated that the shore of the lake extending from the pine barrens at its upper margin to the lowest level attained by the lake is the scene of an ever-changing plant community, an area which is being alternately denuded and reinhabited by a host of plants, the scene of a series of arrested

successions, each succession surviving for only a few years, depending upon the fluctuation in the level of the water table.

In August, 1926, the shore succession probably was as far advanced as it is ever permitted to proceed. At this time two belt transects were made through the zones to determine the qualitative nature of the zones or annual developments of the succession, one on the west side of the lake, the other on the east side. In each transect four zones on the beach were evident marking the annual recessions of the lake from the 1922 high to the 1926 low. Each of these zones was a different plant associates representing later stages in the succession progressing from the lake toward the pine barrens. In addition to these four seral units on the shore, there were two associates in the water. The first of these, the *Callitriche-Potamogeton* associates, occurred in deep water and probably varied little with fluctuations in lake level. The second, the *Eriocaulon-Juncus* associates, was in shallow water and probably migrated somewhat to different elevations in accordance with the variations in lake level. In addition there was one zone in the east transect which, because of the wider beach, was above the usual maximum elevation of the lake and, consequently, presented a much more advanced stage in the succession than the lower zones. It contained such mesic forms as *Vaccinium*, *Betula populifolia*, and *Pinus rigida*. These seven zones were numbered from I to VII beginning with the associates in the deep water. They are diagrammatically represented in Figure 1. Following is a list of the species found in each zone with some accompanying remarks. The nomenclature is according to Gray's Manual of Botany, seventh edition, and the specimens collected during the study are deposited in the Herbarium of the Carnegie Museum at Pittsburgh, Pa.

I. CALLITRICHE-POTAMOGETON ASSOCIATES

Callitriche heterophylla Pursh. *Potamogeton Robbinsii* Oakes.
Potamogeton hybridus Michx.

The first two species were established in the lake at depths of 14 to 15 feet below the surface. Both were commonly found washed ashore, probably loosened from the bottom by fish. They were seen and collected *in situ* only by divers. *P. hybridus* grew in five to six feet of water. This associates represents the initial stage in a hydrarch succession which will ultimately end in a *Pinus rigida* association after the lake has been completely filled by silting and the accumulation of plant remains. This succession cannot develop in the lake until it has been rendered shallow by these processes. However, at the edges of the lake the periodic lowering of the water level with resultant emergence of more or less denuded areas permits the suc-

cession to proceed for a limited time until a recurrence of high water destroys the plant community and initiates a new succession.

II. ERIOCAULON-JUNCUS ASSOCIES

Eriocaulon articulatum (Huds.) Mo- *Juncus dichotomus* Ell.
rong *Juncus pelocarpus* Mey.
Juncus articulatus L.

This zone represented the second stage in the hydrarch succession and occurred in shallow water. In 1926 at its upper limit the water was only a few inches deep. During periods of higher lake levels it was in deeper water. The members of this associates can adjust themselves to various water levels by varying the lengths of their stems.



Fig. 3. Drowning of the Solidago Associates on the west shore of high water in 1929.

III. CYPERUS ASSOCIES

Coreopsis rosea Nutt. *Juncus articulatus* L.
Cyperus sp. *Polygonum Hydropiper* L.
Gratiola aurea Muhl.

This zone which was the third stage in the hydrarch succession represented the first shore zone or the first stage in the secondary succession which was initiated on the denuded beach exposed in the spring of 1926.

It occurred in a very narrow band at the water's edge extending in the west transect only one foot up the shore and in the east transect about four feet from the water.

IV. CYPERUS DENTATUS ASSOCIES

Acalypha gracilens A. Gray

Ambrosia artemisiifolia L.

Coreopsis rosea Nutt.

Cyperus dentatus Torr.

Epilobium coloratum Muhl.

Erechtites hieracifolia (L.) Raf.

Erigeron canadensis L.

Gratiola aurea Muhl.

Juncus articulatus L.

Lactuca canadensis L.

Linaria canadensis (L.) Dumont

Lycopus sessilifolius A. Gray

Polygonum Hydropiper L.

Polygonum Persicaria L.

Quercus coccinea Muench. (seedlings)

Setaria glauca (L.) Beauv.

Stachys hyssopifolia Michx.

Taraxacum erythrospermum Andr.



Fig. 4. Arresting of succession on the east shore in 1929. Inundation of *Solidago* Associes.

Coreopsis rosea Nutt. and *Stachys hyssopifolius* Michx. were subdominant in this associes. This associes represented the second shore zone and occupied the strip of beach exposed in the spring of 1925. It thus represented a stage in the succession one year in advance of the *Cyperus* Associes. Its position is shown in Figure 1.

V. SOLIDAGO ASSOCIES

<i>Agrostis alba</i> L.	<i>Panicum</i> sp.
<i>Agrostis hyemalis</i> (Walt.) B.S.P.	<i>Salix discolor</i> Muhl.
<i>Andropogon virginicus</i> L.	<i>Salix nigra</i> Marsh.
<i>Coreopsis rosea</i> Nutt.	<i>Solidago tenuifolia</i> Pursh.
<i>Gerardia</i> sp.	<i>Stachys hyssopifolia</i> Michx.
<i>Gnaphalium polycephalum</i> Michx.	<i>Strophostyles umbellata</i> (Muhl.) Brit-
<i>Juncus effusus</i> L. (moribund)	ton
<i>Lechea villosa</i> Ell.	<i>Verbascum Thapsus</i> L.
<i>Linaria canadensis</i> (L.) Dumont	<i>Verbena hastata</i> L.
<i>Oenothera muricata</i> L.	

Coreopsis rosea Nutt. was subdominant in this zone. A society of *Strophostyles umbellata* (Muhl.) Britton occurred in one place on the west shore to the exclusion of everything else. This associates represented the third shore zone and occupied the strip of beach exposed in the spring of 1924.

VI. CEPHALANTHUS ASSOCIES

<i>Andropogon virginicus</i> L.	<i>Juniperus virginiana</i> L.
<i>Apocynum cannabinum</i> L.	<i>Lyonia mariana</i> (L.) D. Don.
<i>Asclepias amplexicaulis</i> Sm.	<i>Melampyrum lineare</i> Lam.
<i>Baptisia tinctoria</i> (L.) R. Br.	<i>Myrica carolinensis</i> Mill.
<i>Betula populifolia</i> Marsh.	<i>Panicum Commonsianum</i> Ashe.
<i>Cephalanthus occidentalis</i> L.	<i>Pinus rigida</i> Mill.
<i>Chrysopsis falcata</i> (Pursh.) Ell.	<i>Populus tremuloides</i> Michx.
<i>Chrysopsis mariana</i> (L.) Nutt.	<i>Quercus velutina</i> Lam.
<i>Cyperus filiculmis</i> Vahl.	<i>Robinia Pseudo-Acacia</i> L.
<i>Deschampsia flexuosa</i> (L.) Trin.	<i>Rubus villosus</i> Ait.
<i>Eupatorium hyssopifolium</i> L.	<i>Salix nigra</i> Marsh.
<i>Helianthemum canadense</i> (L.)	<i>Smilax glauca</i> Walt.
Michx.	<i>Solidago odora</i> Ait.
<i>Hypericum perforatum</i> L.	<i>Solidago tenuifolia</i> Pursh.
<i>Juncus articulatus</i> L.	<i>Verbena hastata</i> L.
<i>Juncus dichotomus</i> Ell.	

No species was really dominant in this zone in 1926 but, since some of the specimens of *Cephalanthus* were from ten to fifteen years old, it is probable that over long periods of time this species is the predominant member of the community. While other more mesophytic plants are killed by submergence, *Cephalanthus* probably often survives short periods under water. This area is probably never submerged for any extended time since it is at the level of the maximum elevation of the lake.

It is obvious that this was a more mature stage than any of the preceding as it contained several species of trees, some of which are characteristic of the climax formation of the region. It is highly significant that none of these trees was over four years old. This associates represented the fourth shore zone and occupied the strip of beach exposed in the spring of 1923 following the peak of the rise ending in 1922. The oldest of the above-mentioned trees apparently seeded in the early spring of that year. The upper limit of this zone marks the limit of the high water in 1922.



Fig. 5. Dead *Pinus rigida* on the west shore, 13 to 14 years old, probably established after the high water of 1908 and killed by the high stage in 1922. The living pines to the left were above the latter stage. Photo taken in 1926.

Another significant feature of this zone was a line of dead pitch pines in the lower part of the zone. Counts of growth rings showed that the dead trees in the west transect had died at the age of 13 to 14 years while those in the east transect had lived only 4 to 7 years. The significance of these trees is discussed below in connection with cyclic variation in lake level.

ZONE VII

This zone was apparently above the usual maximum rise of the lake for it showed an advanced stage in the succession. It comprised such mesic forms as birches, maples, oaks, and pines. This zone did not occur in the west transect because on the west side of the lake the steep embankment

bordering the lake extended to the high water line of 1922 or to Zone VI. Since Zone VII was above the level of usual maximum rise, it is of no particular interest in this study and will not be described in detail.

In a reconnaissance of Long Pond, another kettle-hole lake about one mile southwest of Deep Pond, vegetation zones similar to those at the latter lake were found. It is probable that the vegetation changes observed at Deep Pond are more or less characteristic of all the lakes in that general region.

SUCCESSION COMPLEX DURING RISING WATER AS
OBSERVED IN 1929

The presence of the junior author at Deep Pond in 1929 and 1931, three and five years after the first studies were made, afforded an oppor-



Fig. 6. Dead *Pinus rigida* on the east shore 4 to 7 years old, probably established after the high water of 1915 and killed by the 1922 maximum. Photo taken in 1926.

tunity to obtain definite information regarding the effect of the changing lake level upon the vegetation bordering the lake. Following the minimum level of 1926 the lake rose so that by the summer of 1929 the shore line was submerged for a distance of several feet. During that summer the lake continued to rise. This inundation, of course, caused considerable change in the zonal nature of the shore vegetation. There seemed to have been little denudation of the submerged area, possibly because the water

rose rather rapidly and no area was long at the water's edge where the scouring action of the waves is the strongest. Some of the shore zones of 1926 could still be recognized.

Zone I, *Callitriche-Potamogeton* associes, was unchanged as it occurred in deep water and was unaffected by small changes in water level.

Zone II, *Eriocaulon-Juncus* associes, was also practically unaltered. It probably had adjusted itself and migrated somewhat in response to the higher water for it was found in about the same depth of water as in 1926.

Although no changes in floristic composition occurred in the aquatic zones, it was not so with the shore zones. The zones above water had advanced three years in the succession while the recently submerged areas presented a complex structure.

Zone III, *Cyperus* associes, could not be distinguished in 1929 nor could the species constituting it be found. This was a narrow zone at the water's edge in 1926 and probably was quickly submerged by the rising water.

Zone IV, *Cyperus dentatus* associes of 1926, was under water in 1929 and was the scene of opposing processes. This zone was probably represented in 1927 and 1928 by a community similar to the *Solidago* associes of 1926 for this is the next successional step after the *Cyperus dentatus* associes. However, the high water had arrested succession and initiated a new one during 1928 and 1929. Many of the plants of the *Solidago* associes were still thriving but some had disappeared and many more hydric forms had arrived. The following species characteristic of the *Solidago* associes of 1926 were not found in Zone IV in 1929:

Agrostis alba L.

Oenothera muricata L.

Gerardia sp.

Verbascum Thapsus L.

Gnaphalium polycephalum Michx.

The more hydric forms which occurred and which were not characteristic of the *Solidago* associes of 1926 were as follows:

Ambrosia artemisiifolia L.

Hypericum perforatum L.

Bidens frondosa L.

Impatiens alba Nutt.

Cyperus dentatus Torr.

Juncus articulatus L.

Erigeron canadensis (L.) Dumont

Polygonum Hydrophyllum L.

Eupatorium hyssopifolium L.

Polygonum Persicaria L.

Gratiola aurea Muhl.

Viola lanceolata L.

Hypericum canadense L.

A few of the latter group were new arrivals while others probably represented individuals remaining from 1926 when this was the *Cyperus dentatus* associes.

Zone V, the *Solidago* associes of 1926, had progressed to a stage com-

parable to the *Cephalanthus* associates. Although *C. occidentalis* L. had not migrated to this area, other species characteristic of that stage were present. It will not be necessary to list these. Species found in this zone in 1929 which did not occur anywhere on the shore in 1926 are:

<i>Ambrosia artemisiifolia</i> L.	<i>Lactuca canadensis</i> L.
<i>Carex tribuloides</i> Wahl.	<i>Panicum columbianum</i> Scribn.
<i>Cassia nictitans</i> L.	<i>Salix humilis</i> Marsh.
<i>Hypericum canadense</i> L.	

In 1929 the rising lake had partially inundated this zone so that succession was halted in its lower portion. Of the species in this zone characteristic of the *Cephalanthus* associates of 1926 one, *Pinus rigida*, is of particular importance in connection with studies of periodicity in the fluctuation of the lake level discussed below. Small pines had become established and were growing to the water's edge.

Zone VI, the *Cephalanthus* associates of 1926, showed a more advanced state in 1929 by the addition of certain species and by the greater size of the trees and shrubs found in 1926. The additions included:

<i>Acer rubrum</i> L.	<i>Myrica asplenifolia</i> L.
<i>Anaphalis margaritacea</i> (L.) B. & H.	<i>Panax quinquefolia</i> L.
<i>Apocynum androsaemifolium</i> L.	<i>Prunus serotina</i> Ehrh.
<i>Cassia nictitans</i> L.	<i>Pteris aquilina</i> L.
<i>Desmodium marilandicum</i> (L.) DC.	<i>Rhus copallina</i> L.
<i>Epilobium angustifolium</i> L.	<i>Rubus villosus</i> Ait.
<i>Lactuca canadensis</i> L.	<i>Salix pentandra</i> L.
<i>Lechea villosa</i> Ell.	<i>Salix sericea</i> Marsh.
<i>Leucothoë racemosa</i> (L.) A. Gray	<i>Sassafras variifolium</i> (Salsib.) Ktze.
<i>Lysimachia quadrifolia</i> L.	<i>Vaccinium vacillans</i> Kalm.

Zone VII, which occurred above usual high waters and was in the east transect only, was essentially unchanged except for the greater age of its members.

OBSERVATIONS IN 1931

The peak of the rise in lake level was reached late in 1929 for the water was reported receding in the summer of 1930 and was observed doing so in 1931. The level of the lake in the summer of 1931 was 15 inches lower than in the summer of 1929; a strip of shore about 13 feet wide had been re-exposed. At the 1929 maximum the water had not risen to the point which appeared to be the level of the usual maximum rise, i.e., at the upper limit of Zone VI of 1926, but only into Zone V. Consequently, Zone VI and most of Zone V showed in 1931 a continuance of the succession ob-

served in 1926 and 1929 while on the shore below this level the old zones defined at the close of the recession in 1926 were obliterated. A new succession was in progress. Two zones were evident representing the two annual recessions since 1929. The youngest, nearest the water, was similar to Zones III and IV of 1926 with the addition of *Fuirena squarrosa* Michx. and *Drosera longifolia* L. The two-year-old zone was an associates of *Solidago*, *Coreopsis*, and *Eupatorium* and thus resembled Zone V of 1926. The pitch pines growing in Zone V in 1929, which are of especial interest in view of the discussion to follow, were thriving in 1931 about at the level of the maximum elevation of the lake in 1929.

CYCLIC VARIATION IN LAKE LEVEL

The common opinion of local residents that the level of the lakes in the region varies through a seven-year cycle had been largely verified by the observations made at Deer Pond. The campers there reported a maximum rise in 1922. The authors observed a low stage in 1926 followed by a rise with maximum in 1929, seven years after the 1922 maximum. During the years following this peak another recession was observed. In this connection the zones of *Pinus rigida*, dead and living, are of particular importance.

In 1926 two lines of dead pines were found at the lower limit of Zone VI. Since it is known that the water advanced to the upper limit of this zone in 1922 and since the trees appeared to have been dead for about four years, it is fairly safe to assume that they were killed in 1922. Counts of growth rings showed that there were two age groups among these pines. Those in the west transect had died at the age of 13 to 14 years while those in the east transect had lived for only 4 to 7 years. The fact that the oldest trees in each of these groups were 7 and 14 years old, respectively, strongly indicates that the one group lived on the precarious shore area during one cycle of lake-level fluctuation while those of the other lived during two cycles, both being killed by a subsequent maximum rise of unusual intensity in 1922. The following reconstruction has been made upon these assumptions.

An unusual maximum elevation of the lake occurred about the year 1908 which thoroughly denuded the shore to the upper limit of Zone VI (as defined in 1926). During the following recession pines became established on the exposed beach. The water soon returned and reached a maximum in 1915 but of lesser intensity than that of 1908. The pines were killed and subsequently obliterated up to the line of maximum rise which was at the level represented by the lower limit of Zone VI in 1926. Above this level the trees which were then of a maximum age of seven years con-

tinued to thrive through another seven-year cycle. During the lower water stages subsequent to this maximum of 1915 other pines seeded on the exposed beach in various places as in the east transect. When the water reached its unusual maximum in 1922 the pines in the west transect above the 1915 level were of a maximum age of 14 years while those in the east transect below that level were only seven.

One feature of these dead pines which cannot be satisfactorily explained is their occurrence in a definite line rather than in a wide zone as might be expected. No dead trees of lesser years were found lower down on the beach.

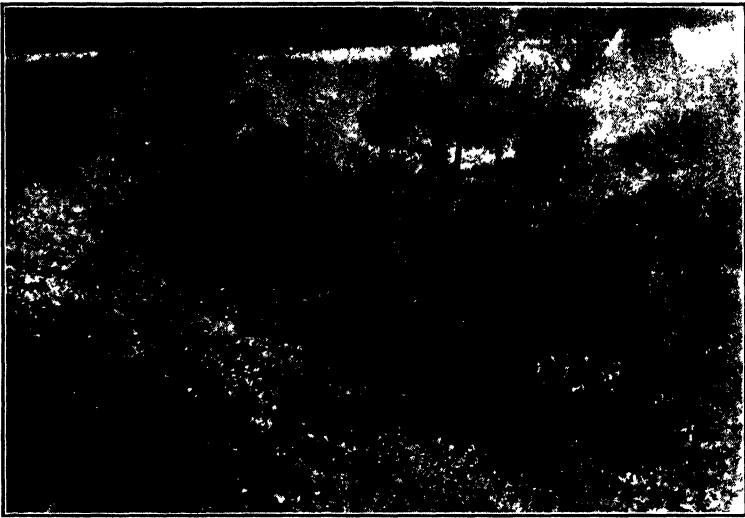


Fig. 7. Living *Pinus rigida* in 1931 slightly below the level at which dead pines occurred in 1926. They were established after the maximum elevation of the lake in 1922 which extended considerably above this; they mark the level of the maximum rise in 1929, and are from 6 to 8 years old. It is highly probable that these trees will be killed by the next elevation of the lake.

However, this does not detract from the reconstruction for it seems that the pines have a tendency to "line up" in a very narrow zone rather than populate a large area. This process was clearly seen in 1929 and 1931. Young pitch pines were found throughout Zone VI in 1926. However, in 1929 there was a definite line of these pines along the water's edge which represented the maximum of the cycle. The younger pines below probably had been washed away. At that time the pines at the water's edge were from 4 to 6 years old. The water did not rise sufficiently to kill these and they were found thriving in 1931 when they were photographed (fig. 7). On the basis of the above assumptions it may be predicted that these trees

will be killed by high water in 1936 when they will show about 14 annual growth rings.

Deep Pond is a kettle-hole lake the level of which is determined by the height of the water table. There seem to have been no records kept of the fluctuation in the level of the ground water in eastern Long Island. However, since this level is dependent upon the rainfall of the general locality, it is of interest to investigate the rainfall records. Figure 8 shows the annual rainfall for the years 1901 to 1930 at Setauket, about eight miles west of Deep Pond as obtained from the reports of the United States Weather Bureau. If there is a seven-year cycle in the fluctuation of the water table there should be a corresponding cycle in the variation in annual rainfall. Maxima and minima in these cycles will not be coincident as there will be a lag in the variation of the water table in response to variations in

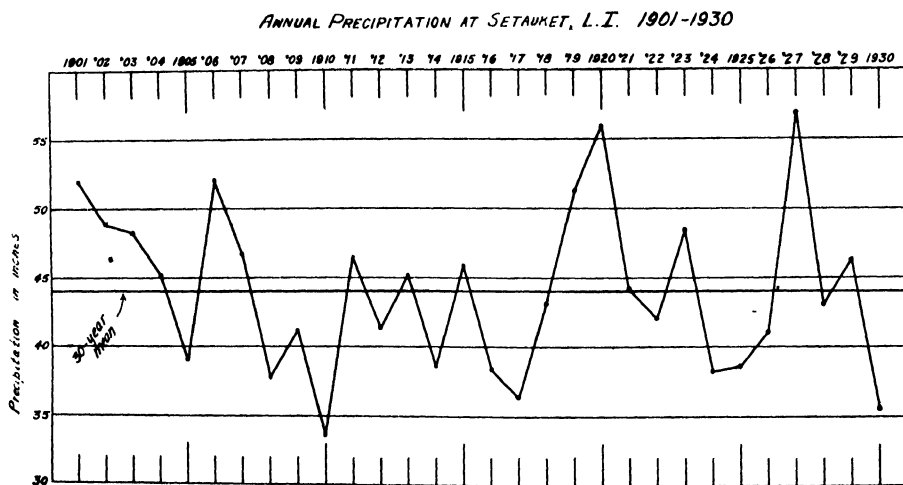


Fig. 8.

rainfall. The definite information available for the lake level for a limited number of years will permit a rough estimate of the amount of this lag.

The earliest authenticated maximum was in 1922. This probably was the result of the maximum rainfall in 1920 (fig. 8) representing a lag of about two years. The lowest level of the lake following this peak was in 1926. This was one and two years, respectively after the low annual precipitations of 1925 and 1924. The next maximum in lake level occurred in 1929. It was of comparatively low intensity and probably represents the effects of the high rainfall in 1927 showing a lag of about two years. Thus, in estimating the comparative level of the lake in past years from the

rainfall data it seems correct to consider a lag of about two years in the fluctuation of the height of the ground water.

In order to satisfactorily explain the occurrence of the pitch pines about the lake shore it was necessary to assume maximum water levels in 1908 and 1915, the one of 1908 of greater severity. It is now desirable to check these assumptions with the rainfall data. If there is a two year lag in the variation in lake level, high waters in those years must have been the result of maxima in the rainfall cycles in 1906 and 1913. Figure 8 shows that 1906 was a year of great rainfall and that 1913 was the last of a series of three fairly wet years. Thus it seems well founded that for the last twenty-five years at least, the rainfall of eastern Long Island has varied in cycles of about seven years causing a similar fluctuation in the water table and level of kettle-hole lakes which in turn has had a pronounced effect upon plant succession at the borders of the lakes.

SUMMARY

1. In 1926 a study of the vegetation bordering Deep Pond, a kettle-hole lake near Wading River, Long Island, showed that on the shore plant succession is periodically arrested and initiated by the fluctuations in the height of the ground water and thus in the level of the lake. Besides two vegetation zones in the water, four shore zones were observed representing four years of succession which occurred during a recession of the lake extending from 1922 to 1926.

2. In 1929 the arresting of one succession and the initiating of another caused by the rising lake level was observed. In 1931 a still later succession was found in progress as the lake once more receded.

3. From a study of zones of dead pitch pines bordering the lake it was deduced that maximum water levels had occurred in 1908 and 1915 and that, at least for the last twenty-five years, the level of the lake fluctuated through a cycle of about seven years. These conclusions were verified by a study of the rainfall records for Setauket, Long Island, which indicated a cyclic variation in rainfall corresponding to the cyclic fluctuation in the water table.

INDEX TO AMERICAN BOTANICAL LITERATURE 1932-1933

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Crops and civilizations¹

E. D. MERRILL

Modern anthropologists in general admit that the beginnings of culture in the history of man took place near the close of the Tertiary. In geologic time this represents somewhere in the neighborhood of 1,000,000 years, but man's even more primitive history probably long antedates this period. At the distant time of 1,000,000 years, man's whole existence was centered on the hunt for food, but even then crude stone implements were in use. For most of the period indicated, man was a primitive nomad. Progress was very slow, and no relatively great steps were made until toward the end of this 1,000,000-year period. Just when various advances were made we do not know, but between 20,000 and 30,000 years ago such innovations as the use of fire, construction of shelters, wearing of clothing, development of sculpture, utilization of bodily ornaments, practice of ceremonies, and formal burial of the dead were established at least among the more progressive peoples of that time. Still man was even then essentially a roving hunter.

Some time approximating 8,000 to 10,000 years ago, there occurred an economic revolution of the greatest significance to man. This was the establishment of agriculture, the domestication of plants and animals, leading to a dependable food supply and thus the formation of permanent settlements, and the development of sedentary life. This economic revolution with its resulting division of labor gave man the opportunity to devote time, energy and attention to other things than merely providing daily food. With agriculture once established, the growth of urban communities, and marked advances in social, civil, political, and ecclesiastical organization, became possible. Thus soon following the beginning of the neolithic age about 10,000 B.C. came the establishment of ceramic industry, the manufacture of textiles, the use of copper, gold, meteoric iron, and, eventually, in the bronze and early iron ages, the development of metallurgy, followed in due time in man's advance by the invention of writing, and other innovations with which we are all more or less familiar.

It seems probable that the domestication of animals preceded the do-

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mestication of plants, and that for a time the more advanced peoples were those who tended their herds. The establishment of permanent agriculture—that is the cultivation of plants—was, however, the great forward step that provided the opportunity for the development of the higher civilizations. Long before the dawn of recorded history, agriculture was a thoroughly established art in various parts of the world, and for untold ages before plants were ever cultivated, man gathered edible seeds, fruits and tubers from wild growing plants, even as primitive peoples do at the present time. We can gain some perspective if we compare the advances made in the past 100 years with those of the past 2,000 years, and again compare man's accomplishments during the past 5,000 years with those of the preceding 15,000 years, and the million or more years preceding the dawn of civilization. The period of great enlightenment has occupied only a very small fraction of man's existence.

The importance of the establishment of agriculture in relation to the progress of mankind cannot be overlooked. It was probably the most significant single advance in man's development. It should be borne in mind that at the dawn of recorded history every basic food plant now grown was already in cultivation and every domestic animal was already in domestication. It is true that modern man has greatly improved both cultivated plants and domesticated animals, but he has added not a single species basic to his food supply to those domesticated by his remote ancestors. We thus owe a tremendous debt to numerous unrecorded individuals, who in remote ages, long before man prepared permanent records, selected from the wild and adapted to their needs through domestication the plants and animals which gave them a permanent food supply and hence paved the way to the development of civilization. So long ago did this happen that these pioneer agriculturists were forgotten long before recorded history commences, for the beginnings of agriculture among all early peoples are lost in mythology. Whether in Mesopotamia or Egypt, in Greece or Rome, in China or among the American Indians, usually the supernatural was invoked to explain this or that basic crop, be it wheat, or barley, or maize, or rice. Among the Egyptians wheat was considered to be the gift of Osiris; among the Romans the gift of Ceres; and we perpetuate this idea today in our common word *cereal*.

It is worthy of more than passing notice that those regions that have actually produced most of our basic food plants and domesticated animals are comparatively restricted, and that it is in these same restricted areas that the ancient higher civilizations developed. All of North America north of Mexico, all of Australia, much of South America, Africa, Europe, and Asia, have contributed little or nothing, and the extreme tropical and

cooler temperate regions have been rather barren fields in originating basic food plants. The important centers of origin of both cultivated plants and domesticated animals have in general been those regions with a Mediterranean type of climate, with no great extremes of heat or cold, and with a reasonably ample and well distributed rainfall or where irrigation could easily be developed; in other words, regions with equable climates. In America the outstanding centers were the highlands of Mexico and of Peru, Bolivia and Ecuador, with secondary centers in Central America and Yucatan; and the food plants basic to these early American civilizations were maize, potato, sweet potato, lima bean, our common field beans, and various indigenous fruits and vegetables. In Eurasia may be listed the Mediterranean basin, Asia Minor, and contiguous areas to the east, limited areas in central Asia, and in parts of India and China. For the Mediterranean basin, Asia Minor and southeastern Asia, the basic food plants were the common cereals, wheat, barley, rye, oats, and certain fruits and vegetables, with such domesticated animals as cattle, horses, swine, sheep and goats, while for India and China perhaps the most important cereal was rice, although others such as millet, sorghum, ragi, coix, and, at an early date, barley and wheat received from the west, with yams and various vegetables and fruits, were used. These limited regions which produced the first, and for that matter most of the cultivated plants and domesticated animals, comprising only a very small fraction of the land surface of the earth, also, significantly, harbored the earliest civilizations. The rest of the world counted for practically nothing, either in the production of basic foods or in providing the rudiments of culture. Among the ancient centers of civilization, only Mesopotamia and Egypt were not the actual homes of the plants on which their life was based. But both regions were contiguous to points of origin of important foods, so both borrowed their agricultural crops from these neighboring lands.

Transportation, however, seldom went farther than to the nearest neighbors. Each ancient center of civilization was also the center for a small group of basic plants which were little known beyond the borders and totally unknown across either ocean. Up to about 1500 A.D. the continental boundaries as between the eastern and western hemispheres governed the dissemination of agricultural plants and animals, and very few cultivated species, none of first importance from the standpoint of food supply, transcended the boundaries of the two hemispheres.

This point leads to another phase of the subject which has not been given the consideration it deserves particularly among anthropologists and ethnologists. This is the vital bearing that this matter has on the origin of early American civilizations. Some authors have assumed and stoutly de-

fended the thesis that the early American civilizations were derived from those of Europe and Asia. Some of the claims are fanciful in the extreme, apparently based largely on preconceived ideas, while others are more logical and have been seriously presented. The Atlantis theory has its ardent supporters, some even going to the extreme of deriving both the Mediterranean and early American cultures from the mythical Atlantis. Even more fanciful are the theories proposed whereby early American civilizations are explained on the basis of the existence of the mythical continent of Mu in the Pacific basin, thus permitting the transmission of Asiatic cultures to America. Others explain certain similarities between the ancient civilizations of Mexico, Peru and Central America and those of Eurasia by various contacts with Europe or Asia, whereby the Old World cultures were transmitted to America. The suggestions, or propositions, include Japanese, Chinese, Greek, Latin, Welsh, Egyptian, Mesopotamian and Polynesian contacts, and some even invoke the lost tribes of Israel. To many of these suggestions serious students of anthropology and ethnology give little or no credence. However, some, apparently representative of that school who would trace all great innovations to a single original source, support the Eurasian-American contact idea on the assumption that architecture, hieroglyphic writing, ecclesiastic, political and civil organizations, etc., either did not or could not originate independently, but having been invented by one people in one place, the art or the idea was transmitted to other peoples by direct or indirect contacts.

Proponents of the Eurasian-American contact theory have rather strangely overlooked the bearing of agriculture on the subject, so let us examine it for them. The closing sentence in de Candolle's classical work on the origin of cultivated plants is as follows: "In the history of cultivated plants I have noticed no traces of communications between the peoples of the old and the new worlds before the discovery of America by Columbus." The fact was so obvious to him, and should be so obvious to anyone who will seriously examine the data, that he did not consider it even necessary to amplify the statement further in connection with any supposed Eurasian influences on early American civilizations.

The number of species of basic cultivated food plants and domesticated animals is not great. For most of them we have very definite information as to the general regions in which they originated. A few cultivated plants have never been found in a wild state, one of the most notable being maize or Indian corn. Others have been so altered in cultivation that we can only approximate what the wild form probably was, as in the case of wheat, and in various vegetables such as those in the genus *Brassica*. If one tabulates the few score species involved as to places of origin, one obtains

a very graphic representation of the truth of de Candolle's statement quoted above. The mere statement that American agriculture, the basis of early American civilizations, was established and maintained until after 1500 absolutely and wholly on native American plants and animals, gains further weight when it is realized that these American basic foods are for the most part produced by plants generically distinct from the food-producing plants of the Old World.

The basic Eurasian food plants are wheat, rye, barley, oats, rice, millet, Italian millet, sorghum, pearl millet, ragi, teff, coix, buckwheat, turnip, cabbage, mustard, radish, beet, parsnip, carrot, onion, leek, garlic, shallot, spinach, egg-plant, lettuce, endive, salsify, celery, globe artichoke, asparagus, pea, cow-pea, chick-pea, pigeon-pea, lentil, soy-bean, broad-bean, hyacinth-bean, asparagus-bean, green-gram, taro, yam, apple, pear, plum, cherry, wine or raisin grape, apricot, peach, prune, olive, fig, almond, persimmon, quince, pomegranate, melon, watermelon, cucumber, sugarcane, banana, cocoanut, orange, lime, lemon, pomelo, date, mango, breadfruit, jak-fruit, rambutan, litchi, longan, lansone, mangosteen and others. The domestic animals include all breeds of cattle, horses, water buffaloes, yaks, sheep, goats, swine, ducks, geese, hens and pigeons. None was known in America before the European contacts following Columbus' voyage in 1492.

The agricultural products basic to American civilizations are fewer than those basic to Eurasian civilizations. They include a single cereal, but this, maize or Indian corn, a most important one; also the potato, sweet potato, lima bean, our common garden and field beans, tomato, pepper, Jerusalem artichoke, sunflower, squash, pumpkin, peanut, quinoa, cassava, arrowroot, chayote, papaya, avocado, cacao, cashew, pineapple, custard apple, sour sop, cherimoya, sapote, sapodilla and others. The domesticated animals were peculiarly few, the llama and alpaca in South America, the turkey in Mexico. None of these was known in Europe or Asia before the voyages of Columbus and of Magellan.

In the light of various theories proposed, postulating the derivation of early American civilizations on the basis of Eurasian contacts and the dissemination of Eurasian ideas and inventions to the less advanced American aborigines, what interpretations shall be placed on the data as presented above? To those who postulate a mythical Atlantis as the ancient center of civilization from which the Mediterranean and early American cultures were derived, for it must be assumed that any highly civilized ancient center must have had a highly developed agriculture, what could have been the agriculture of Atlantis that transmitted to its assumed descendants in the two hemispheres not a single domesticated animal or

cultivated food plant in common? If the continent of Mu ever existed in the Pacific basin, as others assume in explaining these same early American cultures, why did not then the characteristic food plants of Asia reach America with the Asiatic civilizing strain, quite as in more modern times the Aryan peoples took their food and ornamental plants with them when they colonized Malaysia, and where their Sanskritic names for these plants still persist in the Malaysian languages, and quite as the Polynesians took Malaysian plants with them in colonizing Polynesia?

There is another school of anthropologists who support the idea that man reached America from Eurasia as a primitive nomad and that the development of the early American civilizations was purely autochthonous, not in the slightest influenced by the developments in Europe and Asia. The botanical and agricultural evidence is wholly in support of this theory.

Let it be noted that there was one domesticated animal common to both hemispheres previous to the period of European exploration, the common dog. It seems to be a safe assumption that man reached America from Eurasia as a primitive nomad, either bringing the dog with him, or receiving him later over a northern route. He may or may not have left Asia previous to the development of agriculture, although it seems probable that the time of his departure was early enough to antedate any generally established agriculture in Asia. In any case, in the long period involved in his migration over a northern route, in a region inimical to agriculture, not covering months or years, but rather generations, he would have lost all knowledge of agriculture in his life as nomadic hunter and fisher, and later contacts through the north could not possibly have brought him any agricultural knowledge from Asia. As he journeyed further to the south, reaching regions with favorable climatic conditions, and came in contact with wild plants yielding edible fruits or seeds or tubers, his development apparently paralleled that of man in Eurasia: first the gathering of the wild seeds for food, then the primitive cultivation of those plants best adapted to his needs, and finally the evolution of a really high-grade agriculture, the breeding of varieties adaptable to local conditions, the construction of elaborate irrigation systems in our own southwest and in Mexico, and of great terraces in South America. Step by step this paralleled the development of agriculture in the Old World, differing only in the species cultivated.

As agriculture developed it is logical to assume that the higher arts of civilization progressed, quite as in the Old World, including architecture, sculpture, hieroglyphic writing, and political, social, and ecclesiastical organizations. Whatever resemblances there may be between the early high American civilizations in Mexico, Yucatan, Central America and Peru and

those of Europe and Asia they are apparently fortuitous. Having no training as an ethnologist or as an anthropologist and hence having no preconceived ideas on the subject of common origins of arts and crafts, assuming that the early American civilizations were based on agriculture—and an agriculture, as has been shown, based absolutely and wholly on native American plants and animals—I can see no reason why man in America should not have been able, under favorable environmental conditions, to develop an independent civilization, quite as he developed an independent high type of agriculture. If he had borrowed his plants and animals from the Old World, then there would be every reason to believe that he also borrowed his civilization from Eurasia. In the field of biology, including botany and agriculture, the evidence is wholly in support of the theory that man reached America as a primitive nomad and that he here developed his own agriculture and his own civilizations, independent of any Old World contacts. There may have been accidental contacts across the Atlantic; there were relatively late contacts across the Pacific, for the Polynesians unquestionably reached the west coast of America in pre-Columbian times. But such accidental contacts as there were previous to 1492 had no important influences in modifying or shaping the early American civilizations. As in Europe and in Asia, so in America, the early civilizations were essentially from the soil.

Here is a fertile field that has received scant attention from the botanists or the anthropologists. The average systematic botanist looks on cultivated plants as organisms to be ignored, because they are not “native,” and the average botanist in the field never collects a cultivated plant. The average anthropologist has too little interest in, or knowledge of the intricacies of systematic botany to cultivate this field successfully without the cooperation of systematic botanists. Let no one imagine that this is a simple field requiring only observations on which to draw conclusions. I know of no subject more complex, or one where there are more pitfalls to be avoided, among the numerous ones bordering on systematic botany, than this seemingly simple field of ethno-botany. It is an intriguing subject, and one that invites the closer cooperation of the botanist and the anthropologist.

NEW YORK BOTANICAL GARDEN

The Sachs text-book and its influence on the development of botany in America¹

DOUGLAS HOUGHTON CAMPBELL

The middle half of the 19th Century witnessed the rise and development of modern botany, and it was in Germany that the greatest advances were made. From the early studies of Von Mohl and Schleiden, in the 40's to those of Sachs in the 60's, there is a long list of brilliant investigators in morphology and physiology. Sachs' great text-book was first published in 1868, and was an epitome of the results of the researches of such outstanding investigators as Hofmeister, Pringsheim, DeBary, and many others. The text-book was no mere compendium of what had been accomplished up to the time of its publication, but was a store-house of new and important facts based upon the original investigations of the author.

While Sachs is usually regarded as primarily a physiologist, the text-book covers the whole range of botany, and includes many new contributions to morphology and taxonomy which were of great importance, and strongly influenced the work of subsequent students in these fields. He was also greatly interested in the phenomena of sexual reproduction and hybridization and the chapters dealing with these questions, especially the bearing of hybridization on the origin of species, are notable—although of course he could hardly have anticipated the extraordinary discoveries of the geneticists of the present century.

In the preface, the author states that except where it was impossible to obtain material, the book represents the results of his own investigations—a witness to the enormous labor devoted to the writing of the book. The numerous figures are also for the most part original, and have never been surpassed for beauty and accuracy—indeed many of them have served for illustrations in innumerable text-books up to the present time.

This great text-book marks an epoch in the history of botany. The translation into English was undoubtedly the most important factor in the changed attitude toward botanical teaching in both England and America. The first English edition was published in 1875, and was made from the second German edition, published a year earlier. The book was thus made available to botanical students in England and the United States, who for the most part were quite ignorant of the important con-

¹ Invitation address. Memorial Program, Centenary of Julius von Sachs (1832-1897). Joint session of Section G, A.A.A.S., Botanical Society of America, American Society of Plant Physiologists, Mycological Society of America and American Phytopathological Society, December 28, 1932, Atlantic City.

tributions of the German botanists to morphology—physiology. A second enlarged edition, edited by Professor S. H. Vines of Oxford, was published in 1882.

While the most brilliant investigators in Germany were devoting themselves to morphology and physiology—in short to the biological aspects of botany—in England and the United States, the botanists were, with few exceptions, taxonomists, and their interests were almost exclusively with the vascular plants. The influence of such men as Hooker in England, and Gray in America, dominated the teaching of botany in the schools and colleges, and only in exceptional cases were teachers interested in plants as living organisms.

One of these exceptional teachers is worth mentioning, the late Professor W. J. Beal, of the Michigan Agricultural College. Among others of Sachs' students who attained distinction as botanists, was C. E. Bessey, whose *Botany for High Schools and Colleges*, published in 1880, and based to a considerable degree upon the Sachs text, attained a well deserved success, and had a great influence on the trend of both investigation and teaching. This book thus served to introduce the new botany to a host of eager students.

The decade 1870–80 was a notable one in the history of education in the United States. With the establishment of the Johns Hopkins University, for practically the first time the biological aspects of zoology and botany were generally reorganized, and this influence was soon apparent in the courses offered by many of the colleges. Of course there had been exceptional cases earlier where, as in the case of Professor Beal, teachers had an appreciation of plants as living organisms, and not primarily as "specimens," to be named and kept in the herbarium.

Up to this time very few American botanists had studied in Germany. In the early 70's, Dr. W. G. Farlow went to Europe, working under DeBary in Germany and Bornet in France. He was interested especially in the morphology and taxonomy of the algae and fungi, and on his return to America, established at Harvard courses on these which soon attracted many students, especially those interested in the fungi causing plant diseases. In 1878 a professorship of cryptogamic botany was established, to which Dr. Farlow was appointed. There were, at this time, very few special chairs of botany. Even Asa Gray was "Fisher Professor of Natural History." In 1872, Dr. G. L. Goodale was appointed Lecturer in Physiology, and later Professor of Botany.

When I entered the University of Michigan in 1878 I found a well organized introductory course in botany, which might very well have been based on the Sachs text-book. I believe the inauguration of this course was

due to Dr. Mark Harrington who had studied in Germany, and although not primarily a botanist, had been an instructor in this subject.

When I came to college, the work was in charge of the late Professor V. M. Spalding, who, however, at that time ranked only as instructor. Under his direction I was able to carry out a very satisfactory four years' course in botany, and I owe to him my introduction to the work of the great German botanists who at that time were the leaders in botanical investigation. The two names I shall always place first, so far as they directly affected my future work, were Hofmeister and Strasburger. I became greatly interested in Hofmeister's classic studies on the archegoniate plants, which, published eight years before the appearance of Darwin's "Origin of species," clearly demonstrated the genetic connection between Bryophytes and Pteridophytes, shown by a comparative study of their reproduction and embryology. The importance of these investigations was recognized in England, and in 1862 they were translated, and issued under the title, *Hofmeister on the higher Cryptogamia*. It was this book, brought to my attention when I was a student at the University of Michigan, that determined the direction in which my work was to proceed for many years.

As I continued my investigations it was evident that the very crude methods in vogue in our laboratories, were quite inadequate for satisfactory results in the embryological investigations in which I was interested. Little had, as yet, been done in our American botanical laboratories in the study of cytological technique, and it seemed necessary to go abroad for training in modern methods of fixing and staining cytological material. Strasburger was at this time recognized as the great authority, and in 1886 I went to Bonn to work in his laboratory. I may say that the semester spent under his supervision was quite the most important event in my training as a botanist.

As one realizes what men like Hofmeister and Sachs accomplished with the primitive means at their disposal, one may, perhaps, question whether the extraordinary advances in technique at the present day have yielded results of corresponding significance. One feels sometimes as if the perfection of the machine were often considered to be of greater importance than the results for which it was constructed.

Julius von Sachs, the man and the teacher¹

RODNEY H. TRUE

I suppose there is hardly a botanist of middle age here who has not taken long draughts from Sachs' "Textbook of Botany" or from his lectures in Plant Physiology. If there be those of the younger generation who have not had this experience, let me here express the hope that they may not fail to drink of these springs of botanical knowledge and wisdom. I suppose, further, that of those who have handled these well-known volumes, many, like myself, have wished to know something of the powerful personality that gave those books a quality seen in no other author with whom I am acquainted.

Other speakers have the task of appraising the part Sachs will play in the history of plant science; it is my duty to outline here the results of my effort to glimpse that powerful personality that is partially revealed in the writings of Julius von Sachs.

Sachs was born in the capital city of Silesia, Breslau, on October 2, 1832. His birth added the third name to the list of great botanists coming into the world in that city in the same decade. Nathaniel Pringsheim was already nine years old and Ferdinand Cohn was a four-year-old boy when Sachs was born. Curiously enough, it would seem that although the accident of birth might have made a basis of intimacy or at least of acquaintance among them, it is doubtful that the boys were known to each other, and the elder ones certainly exercised little influence on the youngest member of the trio.

Sachs was born into the humble home of an engraver, a home in which financial hardship was the rule and where at times poverty may have entered. But this home did not lack an appreciation of the higher things of life. The father had a keen sense for the beautiful and to his occupation brought the instinct of the artist. Although the family were residents of the city for a greater part of the time, intervals of country living gave to the child an opportunity to see and to love the beauties of nature. He, too, at heart was an artist and out of these early days he brought a quality which blended with his later more confined scientific studies.

In the city he was sent to the Seminarial school in which the training seems to have consisted chiefly in committing lessons to memory in quite uninspiring surroundings. He rebelled against these drab conditions and

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found less profit in his school work than in the training in drawing given by his father. From the 13th to the 16th years of his life, he drew and painted flowers, fungi and other natural objects.

Although the other young botanists-to-be seem not to have come into his life, he was fortunate in making the early acquaintance of two sons of Purkinje, the physiologist, then a member of the faculty in Breslau University. From these boys he learned to collect and press plants, and learning that herbaria were made for their preservation and study, he began to make an herbarium for himself. In this work he had the support again of his father who knew the common names of many of the plants of the region.

Arising with the dawn, he made excursions into the country about the city, and made himself an herbarium of plants that at the age of fourteen he determined for himself from a local flora. Somebody stole his herbarium and inflicted on the boy his first great sorrow. He told his loss to everyone and could not understand the indifference of others to this great disappointment. Goebel, probably relying on an autobiographical account shown to him by Miss Sachs, states that Sachs did not collect plants again until as Professor he assembled a collection for purposes of instruction. This attitude did not arise from any indifference to this phase of his science, since much later he writes in a letter: "To me the so-called *physiologists* to whom the commonest plants of the meadows and gardens are unknown are very unpleasant (unangenehm); these very people are apt to possess very little knowledge of physical things also." He retained throughout his life an interest in the general problems of Systematic Botany.

The seminarists having proved so sterile for the boy, his mother suggested that he should be favored, as none of his brothers before him had been favored because of family poverty, and he enrolled in the Gymnasium. Here he was happy and for five years (1845-'50) was first in his class. He came into friendly terms with one of his teachers, Dr. Rumpelt, and encouraged by him looked forward enthusiastically to scientific pursuits. In spite of the warning of Körber, his botany teacher, that he would never get a groschen for all of his science, he made a collection of skulls and went on his way.

In the year 1848, when he was sixteen years old, dire calamity visited Julius. His father's death was closely followed by that of his mother, and the orphan went to live with an older brother, who out of his own scanty resources provided the boy with an unheated room under the roof. This was gladly accepted and in his attic chamber our young scientist pursued his studies, among his other tasks mastering the contents of Bertholinus' Anatomy written in Latin. Soon, however, affairs became so bad that with

regret he gave up his course in the Gymnasium and planned to become a sailor.

At this critical juncture, when science might have lost one of its future leaders, the acquaintance with the Purkinje family brought to bear a decisive influence that changed his plans. Professor Purkinje had accepted a call to the Czechish University of Prague somewhat before this time, and from his new place of residence offered Julius employment as his private assistant. The lad, now nineteen years of age, went to Purkinje and to Prague. Here he became a student, it is true, but only in so far as his time and effort were not demanded by his employer. It seems that Purkinje paid him poorly and demanded much. He was obliged, as best he could, to eke out his little pay by doing such outside work as he could obtain in order to get a bare living. For six years he was Purkinje's "laboratory slave," six years "rich in self-denial," as one of his biographers says. During these years of overstrain, in order to keep himself nerved up to meet the demands of his master and to accomplish somewhat as a student, the youth, hardly more than a boy, resorted to the overuse of stimulants and formed habits that unfortunately remained with him through life and at times greatly colored his relations with others. It should be said, however, on Purkinje's side that his influence probably did much to turn Sachs' attention toward physiology and gave him command of the methods of the animal physiologist, some of which were later used by him in his work on the physiology of plants. Although there seems to have been little to show for botany in the University of Prague at that time, Sachs left some records of work done during this period. He learned the Czech language, that of Purkinje and of his University, and published his earliest botanical contributions in Purkinje's Czechish periodical—*Ziva*. His first paper on "Growth" appeared in 1853, when Sachs was twenty-one years old and, curiously, was presented in the form of a dialogue. Whether Sachs took this form of composition from philosophical writings that he was then studying with great interest, or whether the teaching instinct so strongly developed in him later led him to choose this type of discourse, is hardly to be decided. At all events, this seems to have been the only instance in which he used this form of presentation.

Some reflection of the philosophical tendency of the times is seen in his next contribution on "Metamorphosis" published a year later. Before the years of his apprenticeship in Purkinje's service expired Sachs had put out two more papers in *Ziva*—one on Starch and another on Transpiration, in 1856. In that year, when twenty-four years old, Sachs took his doctor's degree at Prague.

In view of the weakness of botany in that University at that time, it

seems pretty clear that Sachs proceeded to his goal quite independently of outside stimulus and became a botanist by virtue of his own strong inclination and determination. His *Habilitationschrift* as Privatdocent in the same University followed in 1857, the year in which he left the service of Purkinje. In that year he brought out his paper on the position of lateral roots, using in his study plants grown in water. This circumstance seems to have attracted the attention of the agricultural scientists, although the use of river water as a culture medium for growing plants had been used long before Sachs' time. At all events, in 1859, Sachs was called to his first paying position, that of physiological assistant in the Agricultural Academy of Tharandt, with the special problem set before him of developing a method of growing plants in nutrient solutions. He tarried here for two years, moving in 1861 to the old Poppelsdorf Castle in Bonn, where the Agricultural Institute was then quartered. Here he seems to have made really helpful botanical contacts with Hanstein and with Greyor Kraus. His *Handbuch der Experimental Physiologie*, a pioneer work in which much of his own investigations found place, belongs to this rather brief stay.

Heretofore his work had been that of the laboratory, and the other side of Sachs, the teacher, had found little opportunity for development. His next move, in 1868, to the chair of Botany in the University of Freiburg in Breisgau, as the successor of DeBary, gave him this opportunity. After a year in Freiburg he ended his academic travels by succeeding Nägeli at Würzburg in Bavaria. Here he remained in spite of calls to Heidelberg, Vienna, Berlin, Jena and Munich, and to Würzburg came men from many parts of the world. Two causes seem to have contributed to this concentration in Sachs' laboratories. He had given form and distinction to a new aspect of plant study—Plant Physiology—which can hardly be said to have existed as a defined science before his day. He presented his novelty with a rare charm and power of attraction.

This leads us to an inquiry into those characteristics that made Sachs a distinguished man and one of the most influential teachers known to the history of Botany.

We have already heard somewhat of the hardships that marked his early life, how poverty and ceaseless work had surrounded and wellnigh submerged him. We have heard also how, in spite of them, he had kept his course and achieved as few have achieved. We know that strength gained is measured by obstacles overcome, but sometimes the indomitable will may drive the machine that serves it beyond the limits of safety and finally wear it out. This seems to have happened to Sachs. Taxed beyond the safety limit while yet young, he prematurely found himself handicapped

by severe digestive ills that did much in later years to reduce his activity and to burden his life. Moreover, this tended to influence his attitude toward his fellowmen by making him impatient of their failings, and harsh and at times unjust in his judgment. Gifted himself with a keen and instantaneous insight, he became a severe censor. He was specially impatient of what seemed to him superficial and ill-conceived. He found little to appreciate in the prevailing Platonic ideas of morphology, and although a profound vitalist in his fundamental philosophy, he strove not only to bring plant physiological problems into the region of causality, but sought to bring morphology into that region also. This occasioned sharp collisions with certain of his colleagues. His attack was severe and direct when he caught sight of what he believed to be slipshod. When he met a direct and courageous opponent, his scorn turned to respect, and one who could successfully and boldly overcome his attack not rarely became his firm friend. His scorn was heaped high on one who used as common property, without acknowledging the source, results gained by him. One aspect of this scientific communism that often irritated him was the use of his remarkably accurate and artistically executed drawings that helped to make his "Text-book" and "Physiology" famous, without giving him due credit, and when credit was given he complained that the reader of the work using the illustrations would think that Sachs was a hired artist working for the author. However, one can but ask what botanical writers and students of plants would have lost had they not been able to refer to his well-known figures. It seems probable that this sensitiveness arose out of some kind of complex originating in the early, hard days of his life that put him unduly on the defensive in his later years of pre-eminence. His humble birth was made the basis of stinging remarks during his days with Purkinje, "Bauer" he may have been called, but he failed to draw the sting from the slur, as many would fail now, by adopting a broad, sympathetic view of humankind. Still, one is glad to know that this caste-bound mind must have prized the desired appreciation when, in his later life, he received the coveted title of "Geheimrath" and was ennobled by the King of Bavaria.

In view of the background that I have tried to suggest, it is not difficult to see how he became the great teacher,—probably one of the greatest that Botany has known. Given a keenly sensitive organization, artistic in its fundamental characteristics; given wide reading in philosophy and other fields, and a tendency to seek the general principle, it is clear to see how in his *Lehrkanzel* where he was perfectly free to pour out his wealth of knowledge and enthusiasm to those who eagerly listened, he would feel and transfer the thrill that would make him irresistible. It seems to me

likely that Sachs found a very keen, and in time, longed-for type of satisfaction in this form of self-expression.

For the few who in the beginning perhaps successfully defied and later loved him, he showed another side of his complex and somewhat veiled nature. His assistants felt the cordial warmth, the solicitude for them in the details of the day, and the outflow of confidence, that remained to them a precious possession. The irritable, easily scornful and bitter man seen by so many was the overworked, overstimulated, half-invalid Sachs, driven by the failure of lesser men to appreciate and acknowledge what he had done or to see what to him was so plain. The brilliant teacher, the gentle, considerate friend and companion, the artist-turned-botanist, was the man whom we know best.

I cannot close without a few words regarding Sachs in his literary capacity. It is almost a habit to think of the German scientist as the writer of turbid, involved and difficult sentences, and all of this justly applies to many. None of these characterizes the writing of Sachs. For clarity, coherence and charm, I wish to commend his *Vorlesungen der Pflanzenphysiologie*. The same applies to many of his *Abhandlungen*. When the writer was a student with one of Sachs' most famous botanical children, Pfeffer, he often regretted that the master had not passed on to him that straightforward, lucid style of speaking and writing. However, Pfeffer was worthy of his master.

In view of the tremendous growth that we are now seeing in the old sciences of Physics and Astronomy, it would be ill-advised to say that the advance of human understanding may not later cause another epochal chapter to be written into the history of Botany. Perhaps with the application of the new methods now being developed in Physics and Chemistry, someone may add another great area to botanical knowledge. Perhaps another Sachs may appear.

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Sachs, the last of botanical epitomists¹

CHARLES E. ALLEN

An introductory reference may be pardoned to a topic already discussed today by one who speaks with authority. The development of botanical knowledge during the nineteenth century is recorded in successive editions of three great German textbooks. Schleiden's text, which began to appear in 1842, apart from its important polemic aspect, aimed to present a comprehensive exposition of the science. The precedent thus established was to be scrupulously observed by Schleiden's German successors. Twenty-six years later came the first edition of Sachs' *Lehrbuch*. That its author approached more nearly the ideal, that in organization, in proportion of emphasis, in tolerant yet critical comprehension of others' contributions his text far excelled—these facts but emphasize the significance of his own comment, that the difference between Schleiden's "and all previous textbooks is the difference between day and night." Thanks to Schleiden, argument, exhortation, and denunciation were no longer required to establish botany on the basis of an inductive science. It remained, however, for Sachs to present a summary, satisfying, in its completeness and symmetry, his own critical artistic sense, a summary which, allowing for the contemporary state of knowledge, has never been excelled.

When, after another twenty-six years, a third—the *Bonner Lehrbuch*—appeared, it is noteworthy that its production involved the collaboration of four specialists. That such collaboration was needed is an added indication of Sachs' position in the history of botany. Not only had he, while engaged in providing formative stuffs for the still wholly meristematic shoot of plant physiology, organized and epitomized the botanical knowledge of his day; he represented the climax and marked the close of a period in which such mastery by a single mind was possible. Previous to the transitional stage personified, as it were, by him, there were masters of botany. Since, there have been masters of special botanical fields. "General botany," thought of as a term describing the activities of an individual, was thereafter to be, like "general biology" or the later-invented "general physiology," meaningless save as an expression of pious aspiration, or as a claim of transcendent importance for the user's particular line of interest.

When, after successive revisions of the *Lehrbuch*, Sachs could not, despite his fondness for arduous labor, drive himself to the preparation of

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a new edition, he turned to the writing on a freer plan of his *Vorlesungen über Pflanzenphysiologie*. His work as a physiologist, also, has been covered today by one who knows his pH, and is not to be detailed here. But it will be permissible to note that the *Vorlesungen* represents a natural development of the *Lehrbuch*, covering a large proportion of the same subject matter, and illustrating Sachs' views as to the proper content of plant physiology. Nearly a fourth of the first edition of the *Vorlesungen* (1882) is devoted to organography, including the morphology and anatomy of vegetative parts, and cell structure. Somewhat more than one tenth is given to reproduction with extended descriptions of gametogenesis and syngamy, and discussions of devices insuring self- or cross-pollination, of apogamy, and of the effects of hybridization. It may, to be sure, be suggested that the so-inclusive treatment of his subject was the expression of a view persisting from the days before his own contributions had increased and organized physiological knowledge. When, as a young *Privatdozent*, Sachs first announced a course of lectures on plant physiology, a chemical friend inquired (of course in courteous Teutonic phraseology): "How do you get that way? You can cover the subject in two hours." And Goebel, relating the incident, adds that, considering the period, the chemical friend was not so far astray. Whatever the explanation may be, Sachs' lectures on plant physiology evidence, like his textbook, his power of organization and summary within an extremely broad field.

With Sachs' *Vorlesungen* may be compared the first edition of Pfeffer's *Pflanzenphysiologie*, which, although representing a younger viewpoint, appeared a year earlier. Pfeffer has nothing to say of organography, unless a brief description of protoplasmic structure be therein included, and nothing of reproduction save a paragraph discussing the movements of archegoniate antherozoids. The difference in inclusiveness and the shift of emphasis as between master and student are significant. Sachs, throughout his active life, stressed the unity of structure and function as varied aspects of a single problem. To Pfeffer, physiology was *Stoffwechsel und Kraftwechsel*. Even this definition might have covered the complex of phenomena included under, or related to, reproduction; but Pfeffer did not so interpret it. The latter's predominance in the physiological field after Sachs had passed from the scene determined a limitation of the activities of those calling themselves plant physiologists much narrower than any possible to the mind of Sachs. The effect of this limitation is illustrated by a sentence in a much later textbook of plant physiology prepared by one of Pfeffer's American students: "That topic [reproduction] is relegated to morphology, since the purely physiological processes are relatively simple, so far as known, and very much alike."

Doubtless, one reason for Pfeffer's willingness thus to limit the subject matter of physiology lay in the appearance of the new school of cytologists who were rapidly advancing the knowledge of reproductive processes, and who, as it happened, were predominantly men of morphological and anatomical training. Had Sachs' comprehensive, rather than Pfeffer's more limited, view as to the proper scope of plant physiology prevailed, meetings of physiologists might now be listening to accounts of chromonemata, genic localization, and segmental interchange. It is eminently fitting that present-day plant physiologists revere the memory of Pfeffer.

The breadth of Sachs' interest in, and his inclusive mastery of, botanical subject matter are likewise evidenced by the variety of problems outside the range of plant physiology, broadly or narrowly interpreted, to which his own researches and those of his students contributed. His interest in strict morphology, early illustrated by the papers on *Crucibulum* and *Collema*, appears in his later discussions of "architypes," and in his extensive investigation, recorded in the *Lehrbuch*, of the structures of archegoniates. Inherent throughout his writings, and repeatedly expressly stated, was the conviction already referred to, that structure and function must be considered together. Down to the time of writing the very latest of his published papers he was attempting to disentangle and elucidate the factors causal to the development of form; discriminating more and more sharply between environmental stimuli and internal factors, the latter identified by such terms as *Gestaltungstrieb*, nowadays more orthodoxly, if not more illuminatingly, embodied in the concept of the genotype. One contribution to this problem of the causation of development was the doctrine of formative stuffs; another, the discussion of the bearing of growth tendencies upon the appearance respectively of radial or of bilateral symmetry. In the field of causal morphology his tradition was continued by his student Goebel, as another student, Pfeffer, represented a continuation of Sachs' interest in *Stoff- und Kraftwechsel*.

His morphological studies bore close relation to, perhaps were in part an outgrowth of, his concern with problems of relationship, the fascination of which he admitted having felt from youth. Goebel quotes him as saying that he had followed physiology because it seemed to him that "the final problems of systematics are to be solved only by physiological methods." These questions of relationship—"the final problems of systematics"—inevitably led him, as a contemporary of Darwin, into discussions of organic evolution, just as the problems of causal morphology drew him to the consideration of the bases of inheritance and variation. His change in attitude toward Darwin between the time of the appearance of the German, and that of the publication of the English, edition of his history is well

known. While accepting the doctrine of descent, Sachs abandoned faith in all attempts, including especially the theory of natural selection, to explain the evolutionary process. "The natural system," he said, "is explicable only by descent; how descent is to be explained, nobody knows."

In the field of inheritance, the doctrine of the continuity of the embryonic substance in plants antedated, as has often been pointed out, Weismann's adoption of the distinct, but related, hypothesis of the continuity of the germplasm. This embryonic substance of meristematic cells, Sachs said, "has remained continuously alive since the beginning of organic life upon the earth, constantly renewing itself, persisting through the changes to which all organisms are subject, as well as through the endless alternation of life and death." After the establishment of the chromosome theory by Hertwig and Strasburger, Sachs, like Weismann, accepted and included in his conception the preponderant influence of the nuclear substances; although he stated, more clearly than some of his contemporaries, the significance of the cytoplasm and of its interaction with the karyoplasm in developmental processes.

An early statement of the energid concept contains an anticipation of Richard Hertwig's theory of nucleocytoplasmic relations. It may not be too fanciful to suggest that in the formulation of this concept, not fully confirmed by later studies of the organization of multinucleate cells, Sachs was a victim of the intellectual limitation which inhibits our analysis of phenomena of almost any type save in terms of small and ever smaller units. A logical development of the fruitful ideas basic to the energid hypothesis was the study by Amelung, at Sachs' instigation, of average cell sizes and of the relation of cell size to organ and body size. A sentence from one of his letters to Noll is suggestive in this connection: "The time will come, as I have often said, when the deepest secrets of nature will be sought, not by means of metallic contrivances, but in the energids themselves."

Another problem to which Sachs repeatedly turned was that of the laws which govern the sequence of cell divisions and the resultant intersections of partition walls. Although the question had already engaged the attention of Hofmeister, the conceptions developed by Sachs supplied the real starting-point for later work. This study in turn led to a consideration of the relation between growth and cell division. His insistence upon the unity of the multicellular organism as a regulatory factor in the determination of directions of growth and planes of division led to the enunciation of what has been considered one of the many forms of the "organismal" theory. However, it is not without significance that maturer consideration led him far enough away from his former somewhat mystical attitude to

enable him to point out that "the total form of the plant and the succession of its organs are determined by the energids alone."

But it is as a historian of botany that Sachs' characteristic power of summary and epitome is most evident. His *History of Botany from 1530 to 1860* is still, and promises for many years to remain, the only work in its class. Although nominally limited to the dates mentioned, there are expositions, brief but enlightening, of progress from ancient times to the beginning of modern botany. So general has been the recognition of his erudition, thoroughness, skill, and judgment in this presentation of the growth of botanical knowledge through the centuries, that an attempt at further comment would be superfluous. That errors of fact and of judgment should have been discovered is not surprising; it is surprising that errors were so few.

Sachs' purpose cannot be too clearly recognized in any critical evaluation of his *History*. He deliberately refrained from cataloguing discoveries of facts save "when they could be shown to have promoted the development of the science." This recalls an earlier expression of his attitude in the preparation of his *Lehrbuch* which, he said, was intended to familiarize the beginner "not only with the most important facts at present established concerning the life of plants, but also with the theories and problems with which botanical investigation is at present chiefly concerned." In like vein was his insistence that "scientific merit belongs only to the man who clearly recognizes the theoretical importance of an idea, and endeavors to make use of it for the promotion of his science."

There is, of course, another real aspect of the history of a science. In this aspect the historian seeks to trace the accumulation of the knowledge of facts, as well as the process of elimination of those accumulated "facts" which are not facts. This type of study of the development of a branch of knowledge has its own particular value; but it was not the type of study that appealed to Sachs. To him, the true aim of the history of a science was "to discover the first dawning of scientific ideas and to follow them as they developed into comprehensive theories." Considered from this standpoint, his *History* speaks as nearly the last word as any historical work possibly can.

The point at which Sachs closed his chronicle marks approximately the end of the period within which one writer could successfully summarize botanical accomplishments with an important part of which he was contemporary. In the writing of history also, then, Sachs was the last of botanical epitomists. In a remote future, after many workers have reviewed the history of developments in their special lines, and when time has obscured much of passing interest that bulks so large while it is passing, some

writer, assimilating the results of these studies of phases of the science of which he knows personally relatively little, may record the development of botany as a whole from 1860 to 1960. But such a one will not be doing the work that was done by Sachs.

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A carpological enigma

H. H. RUSBY

(WITH PLATE 20)

In the summer of 1921, while on the Mulford Expedition, Dr. O. E. White collected, in the vicinity of Rurrenabaque, Bolivia, a leafy and a fruiting twig, the edible fruit of which possesses a structural peculiarity not heretofore described, so far as I can ascertain, and the morphology of which I am unable to explain.

The plant is quite clearly a member of the Myristicaceae, but does not fit into any described genus. The only information accompanying the specimen is Dr. White's notation. "*Durasno del monte. Mui rico*," which I interpret as "Mountain or Wild Peach. Very rich." Whether it is the pericarp or the seed that is eaten and is "very rich," is not stated. The fruits are apparently immature, and not fully grown. They are paniculate and pendulous on stout and tough branchlets and pedicels, and the base is slightly umbilicate at the stout attachment. The fruit is about as large as a good sized peach, which it closely resembles, the surface being downy as in the peach. It also closely resembles the fruit of the nutmeg. There is no sign of a suture, and in its present immature state, no indication of dehiscence. The sarcocarp is about 6 mm. thick and is not very tender or fleshy. I assume that it has become contracted and hardened by its long immersion in formaldehyde, and that in a mature and fresh condition, it might be much more attractive for eating. The putamen is 1.5 mm. thick and is at present adherent to the sarcocarp. It is crustaceous in texture and of a white color throughout, and its inner surface is smooth and shining. The solitary seed is erect and atropous and is irregularly globose. It entirely fills the cavity, being about 4 cm. long and broad. It is white in color and has a broad, brown, flat or slightly impressed hilum. Running from the hilum are a number of shallow and irregular grooves and ridges. There is no aril, but its strange and inexplicable feature is the partial envelopment of the seed in a leaf-like organ that originates from the tip of the pericarp. From the material at hand, I am unable to determine from which layer of the pericarp it originates. It has a short and rather stout dark-colored petiole, which is continued into a stout midrib that curves along the surface to the hilum and sends a number of weak branches out into the thin and hyaline lamina that partially surrounds the seed. The surfaces of the leaf are entirely free from both the seed and the endocarp. The seed consists mostly of fleshy endosperm, with no separable testa or tegumen. This white endosperm is irregularly crumpled but is firm and compact, and appears as though it might well be edible, like a nut. The

large centric embryo is broad, thin but tough, and strongly and irregularly crumpled. It has a well-formed short, stout, dark-colored and shining caulicle. A twig bearing two leaves is present. These are alternate and without indication of stipules. The petioles are short, stout and slightly twisted as though they might have served for support, though this is conjectural. They are broadly ovate, obtuse, entire, thin but tough, pale-green and glabrous, the venation rather sparse but strong and prominent, giving the leaf a rugose appearance.

Both fruit and seed manifest affinity with the Myristicaceae, but differ in the absence of an aril, and in the presence of the intra-carpellary leaf-structure here described. I have been unable to find any other family to which it could have been so well referred.

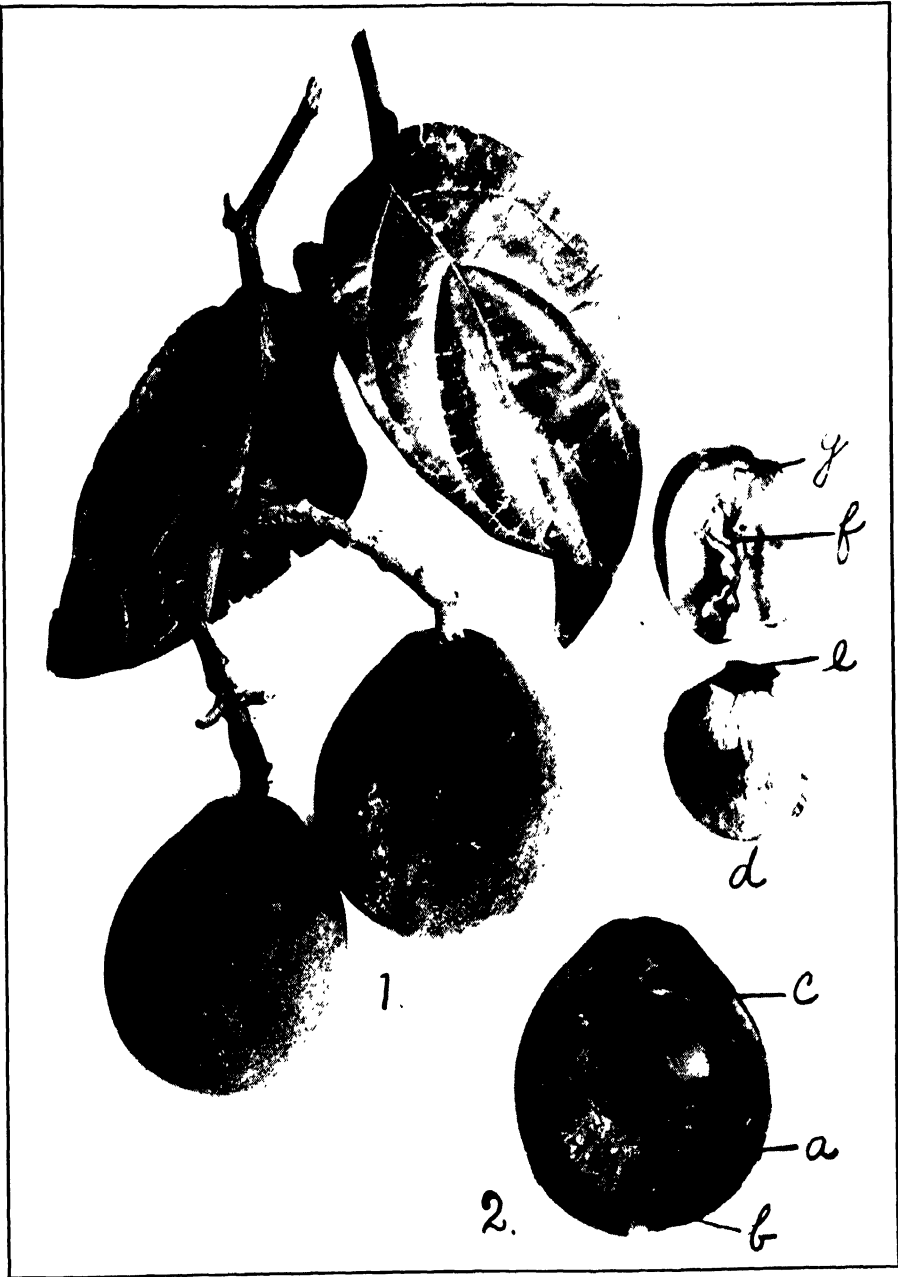
If one could imagine that the leaf-like appendage to a stigma, such as we see in *Stigmaphyllon*, had become reflexed and involved as a lining to the ovary, we should have an exact picture of the position of this unique intra-carpellary appendage.

Although apparently no such genus has been described, it seems undesirable to propose a name for this plant until we have more complete information concerning it.

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Explanation of plate 20

Durasno del Monte (Myristicaceae) Fig. 1, leafy and fruiting twigs; Fig. 2, longitudinal section of fruit; a, petiole of intracarpellary leaf; b, point of origin at tip of pericarp; c, portion of lamina; d, exterior of seed; e, hilum; f, crumpled cotyledons of embryo; g, tip of caulicle near micropyle, (slightly reduced).



RUSBY CARPOLOGICAL ENIGMA

Plantae Krukovianae

H. A. GLEASON and A. C. SMITH

(WITH PLATES 21, 22)

During the last few months of 1931 Mr. B. A. Krukoff made collections, largely of forest trees, in Amazonian Brazil. The collections were chiefly from two regions: the plateau between the Xingu and Tapajos Rivers in the State of Pará, and the region of the Machado River (Madeira River system) in the State of Matto Grosso. The present paper is planned to describe the new species collected by him. All types are deposited in the herbarium of the New York Botanical Garden. The authors wish to thank the specialists E. P. Killip, E. C. Leonard, H. N. Moldenke, C. V. Morton, P. C. Standley, and R. E. Woodson, for their cooperation in determining and describing certain specimens.

ARACEAE

Philodendron Krukovii Gleason, sp. nov. Caules graciles epiphytici subteretes glabri ad laterem unum biangulati et leviter sulcati, internodiis ad 25 mm. longis; petioli recti 4–7 cm. longi, e basi expansa caulem amplectente contracti, superne 3–4 mm. lati, lateribus parallelis, supra plani vel leviter canaliculati subtus rotundati vel paullum angulati anguste alati; alae vaginales cartilagineae, infra basin laminae supra petiolum confluentes et in ligulam obtusam 1 mm. longam productae; pars petioli libera 2 mm. longa; laminae subcoriaceae opacae virides lanceolato-oblongae subfalcatae inequilaterae 14–24 cm. longae 35–65 mm. latae, latere dextro quam sinistro fere $1/2$ latiore, infra medium ad basin rotundatam sensim angustatae, apice acuminatae; venae laterales I in quoque latere ad 9 a costa sub angulo 70° divergentes, ultra medium sursum curvatae et prope marginem tenuiores cum aliis conjunctae, supra planae obscurae subtus stramineae paullum elevatae; venae laterales II numerosae creberrime parallelae inter se circa 1 mm. distantes, prope marginem a venis I non distinguendae et cum eis conjunctae, supra virides obscurae subtus stramineae, utrinque paullulum elevatae, venulae numerosae; pedunculus solitarius terminalis crassus 1 cm. longus purpureo-brunneus; spatha lanceolata supra basin 35 mm. lata 9 cm. longa, ad apicem obtusa vel subrotundata et appendicula tereti 5 mm. longa ornata, spadice aequans; spadix circa 8 mm. stipitatus subteres ad basin atropurpuream vix incrassatus, ad 7 mm. diametro, superne flavo-brunneus sensim angustatus.

Type, *Krukoff 1408*, collected Nov. 23, 1931, near Tabajara, upper Machado River region, State of Matto Grosso. A member of Sect. *Pteromischum* Schott, it finds its nearest relative in *P. guttiferum* Kunth, in which the leaves are proportionately twice as wide, of an ovate-lanceolate type, and the petiole much more broadly winged.

RAPATEACEAE

Saxo-Fridericia australis Gleason, sp. nov. Foliorum vaginae basales lineari-lanceolatae ultra 34 cm. longae et 3 cm. latae, superne in petiolum gradatim angustatae, in parte superiori marginis unae spinuloso-serratae, in margine altera integrae; petiolus inter laminam et vaginam haud evolutus 7 mm. diam. glaber, marginibus anguste alatis et spinuloso-denticulatis, spinulis subulatis rectis patentibus; lamina lineari-lanceolata ad 165 cm. longa, latere uno 4.5 cm. lato basi longe cuneato, altero 3.5 cm. lato et 1–9 cm. altius oriente, ad marginem in parte inferiori spinuloso-denticulata velut in petiolo, superiori minutissime adpresso-spinulosa, apice longissime acuminata, supra glabra, vena media canaliculata 5 mm. lata, subtus concolor, costa crassa semitereti, venis lateralibus in quoque latere 7 vel 12, lineis albidis transversalibus divisus et anastomosantibus creberrime notata; pedunculus ultra 40 cm. longus gracilis, in sicco angulatus, glaber, superne vix incrassatus vel ad 8 mm. latus; capitulum fructiferum globosum 3 cm. diam.; bracteae jam post maturitatem in speciminibus plurimis delapsae, in una sola capitulum partim obtegentes; capitulum globosum multiflorum 3 cm. diam.; flores singuli cum bracteolis turbinati vel obconici 12 mm. longi; bracteolae circ. 30 lineari-clavatae acutae vel breviter acuminatae, exteriores 1-nerviae 7 mm. longae in parte superiori 0.8 mm. latae, interiores 3–5-nerviae 10 mm. longae 1.8 mm. latae, omnes adpressae induratae; sepala lanceolato-oblonga 11 mm. longa 3.3 mm. lata 5-nervia basi scariosa apice indurata acuminata; capsula ellipsoidea 7 mm. longa in rostrum brevem abrupte angustata obscure 3-angulata loculicida 3-locularis; semen 1 reniforme paullum complanatum 5 mm. longum glabrum medio affixum; antherae post anthesin persistentes e calyce exsertae lineari-subulatae 4.5 mm. longae, ad apicem in apiculam linearem 0.4 mm. longam subito angustatae, infra apicem poris 2 elongatis vel rimulis 2 brevibus 0.6 mm. longis dehiscentes.

Type, *Krukoff 1065*, collected Sept. 10, 1931, on "terra firma" on the plateau between the Xingu and Tapajos Rivers, State of Pará. The specimens are unfortunately past anthesis; in one the remains of the typical involucre persist and in a few withered anthers still persist on the fruiting heads. The habit of the large leaves, and the structure of the involucre and anthers leave no doubt of its generic affinity. The characters of the genus and its three species hitherto known were well summarized by Koernicke in 1872. *S. regalis*, of the Roraima region, has well imbricated bracteoles gradually increasing in length from the outer to the inner; the other two have bracteoles of nearly the same length and in that respect agree with ours. *S. subcordata* has leaves cordate at base, while *S. aculeata*, of French Guiana, further resembles ours in leaves narrowed to the base. The last species differs from ours in the margin of the petiole and leaves, which are spinulose-denticulate throughout their entire length with tri-

angular incurved teeth, and in its shorter peduncle strongly expanded beneath the head. The fruit of *S. aculeata* was unknown to Koernicke. Its ovary contains two ovules in each locule, in which it agrees with *S. australis*.

Few species of the family are known from south of the Amazon, and the present collection extends the range of the genus by about 500 miles.

MARANTACEAE

Ischnosiphon flagellatus Gleason, sp. nov. Caulis simplex erectus herbaceus 60 cm. altus, basi vaginis obtectus, vaginis lanceolatis adpressis pallide brunneis vel stramineis longitudinaliter venosis ab inferioribus 15 mm. longis ad superiores 10 cm. longas gradatim accrescentibus; vaginae foliorum ad 13 cm. longae internodia omnino tegentes, minute pubescentes praecipue ultra medium, ad apicem in linea pubescenti cartilaginea obliqua a basi petioli ad margines vaginae extensa et prope marginem setis 2 erectis ad 10 mm. longis ornata terminantes, ultra apicem ligulam intrapetiolarem 6–8 mm. longam ovato-oblongam integram glabram gerentes; petioli crassi complanati dense puberuli 2 mm. longi; laminae foliorum inferiorum ovatae 9 cm. longae 4 cm. latae basi rotundatae apice acutae, superiorum lanceolato-ellipticae ad 18 cm. longae 6 cm. latae acuminatae, basi subrotundatae vel late cuneatae, omnes ad venam mediam minutissime puberulae ceterum utrinque glabrae, apice rectae; spica ex axilla folii superioris solitaria sessilis jam a bractea singula straminea superne spiraliter torta omnino oblecta; flores nondum evoluti.

Type, *Krukoff 1307*, collected Nov. 7, 1931, on "terra firma" at Calama, Madeira River region, State of Amazonas. *I. flagellatus* is apparently related to *I. surinamensis* (Miq.) Koernicke, but differs from it and all other described species in the structure of the ligule.

MYRISTICACEAE

Virola elliptica A. C. Smith, sp. nov. Arbor 20–25 m. altus, prope basin 0.6–0.8 m. diametro; ramulis rectis teretibus glabris, in sicco rugosis nigrescentibus; petiolis velut ramulis, 7–9 mm. longis, 1.5 mm. diametro, inferne teretibus superne canaliculatis; laminis coriaceis oblongis, 12–20 cm. longis, 3–5 cm. latis, basi cuneatis, apice breviter acuminatis vel acutis, margine integris et leviter recurvatis, utrinque glabris, supra nitidis saepe subnigrescentibus, subtus fusciscentibus, costa supra plana vel leviter impressa subtus prominente, nervis secundariis 18–22-jugis subrectis prope marginem arcuatis conjunctis, supra peracute impressis subtus elevatis, venulis immersis; inflorescentiis axillaribus in fructu ubique glabris quam foliis paullo brevioribus; fructibus breviter pedicellatis oblongo-ovoideis, maturitate 3 cm. longis et 1.6 cm. latis, longitudinaliter acute circumcarinatis; pericarpio sublignoso saepe rugoso, arillo fere ad basin laciniato, semine ovoideo, 20–30 mm. longo, 13–14 mm. lato.

Type, *Krukoff 1333*, collected Nov. 12, 1931, on "terra firma" near Tabajara, upper Machado River region, State of Matto Grosso. Like other Brazilian species of the genus, it is locally known as "Ucuuba." It is allied to *V. carinata* (Benth.) Warb., from which it differs by having the secondary veins acutely rather than bluntly impressed, and by having the fruit elliptic. The fruit of the present species is about twice as long as broad, while that of *V. carinata* is subglobose and smaller. *Krukoff 1496*, also from the vicinity of Tabajara, is identical with *1333* in foliage, but differs by having its fruits larger (often 5 cm. \times 2 cm. at maturity) and with the longitudinal ridge less prominent. In view of the similarity of these two specimens in all other features, I am inclined to consider them one species. However, future collection of the flowers may indicate that two species are represented.

Two species of *Iryanthera* of which the fruit has not previously been described were collected by Krukoff. The following notes may be added to descriptions of the species:

IRYANTHERA JURUENSIS Warb. Fruiting inflorescence 8–9 cm. long; fruit short-pedicelled (pedicel 5–10 mm. long), transversely elliptic, about 3.5 cm. thick and 5 cm. on the long axis, substipitate at base, rounded at apex; pericarp woody, very rugose, about 7 mm. thick, vertically dehiscent; aril entire; seed transversely elliptic, about 33 mm. \times 18 mm.

Matto Grosso: near Tabajara, upper Machado River region, *Krukoff 1391*. Our specimen is a tree about 30 meters high and 1 meter in diameter, breast high, with the local name of "Ucuuba vermelha." The collector notes that the inner bark gives a thick red exudation.

IRYANTHERA ULEI Warb. Fruiting inflorescences fasciculate, 5–7 cm. long; fruit pedicellate (pedicels 4–6 mm. long), transversely elliptic, about 14 mm. thick and 25 mm. on the long axis; pericarp rugose, about 1 mm. thick, vertically dehiscent; aril entire; seed transversely elliptic, about 23 mm. \times 12 mm.

Amazonas: near Calama, Madeira River region, *Krukoff 1298*. The collector notes that the specimen is a tree about 16 meters high and 0.3 meters in diameter, breast high; a local name is "Ucuuba rana," and the seeds are used for extraction of oil.

MONIMIACEAE

Siparuna Krukovii A. C. Smith, sp. nov. Frutex circiter 6 m. altus; ramulis subteretibus fuscis, parce stellulato-pilosis mox glabrescentibus; petiolis oppositis gracilibus subteretibus 5–7 mm. longis, velut ramulis novellis pilosis; laminis papyraceis oblongo-ovatis, 10–14 cm. longis, 4.5–5.5 cm. latis, basi obtusis vel subacutis, apice acuminatis (acumine 5–15 mm. longo), margine integris saepe sinuatis, utrinque glabris (costa saepe puberula), copiose pel-

lucido-punctatis, pinnatinerviis, nervis lateralibus 5–7-jugis arcuato-adscendentibus prope marginem anastomosantibus, cum costa supra leviter elevatis subtus prominentibus, venulis copiose reticulatis elevatis vel planis; inflorescentiis ♀ cymosis, cymis in foliorum axillis 1 vel 2 paucifloris 12–20 mm. longis, ubique parce cinereo-stellulato-puberulis; pedicellis 2.5–4.5 mm. longis; floribus ♀ subrugosis, maturitate 2 mm. diametro; receptaculis subglobosis, tepalis omnino obsoletis; velo glabro conico-elevato circiter 0.5 mm. longo, ore minuto; stylis ad apices firme connatis, 0.5–0.7 mm. exsertis; carpellis plerumque 5 vel 6.

Type, *Krukoff 1682*, collected Dec. 27, 1931, on “terra firma” near the source of the Jatuarana River, Machado River region, State of Matto Grosso. It is related to *S. micrantha* A. DC., from which it differs by having the leaves proportionately broader and with fewer lateral nerves, and the styles, which are connate to the apices, strongly exserted.

ROSACEAE

Parinarium Krukovii Gleason, sp. nov. Arbor, ramulis teretibus rugosis glabris griseis; petioli vetustiores 4–6 mm. longi glabri rugosi eglandulosi, supra canaliculati; foliorum laminae tenuiter coriaceae anguste elliptico-oblongae 6–9 cm. longae 2–3 cm. latae, basi acutiusculae, ad apicem acutam abrupte acuminatae, supra glabrae lucidae costa prominente, venis secundariis planis obscuris, venulis arctissime reticulatis et levissime impressis, subtus ad costam validam prominentem et venas secundarias utrinque 10–12 sub angulo 50° orientes subrectas prope marginem curvato-adscendentes glabrae, ad paginam tenuissime canescentes; panicula fructifera terminalis pauciramosa foliis brevior axibus jam velut ramulis lignosis; drupa fusca ellipsoidea ad 25 mm. longa, apice rotundata, saepe subfalcata.

Type, *Krukoff 1362*, collected Nov. 15, 1931, on “terra firma,” near Tabajara, upper Machado River region, State of Matto Grosso. It is related to *P. brasiliense* Hook. f., *P. Pohlii* Hook. f., and *P. Glaziovianum* Warm., differing from all of them in the glabrous branches, the glabrous midvein, and the lack of conspicuous pubescence on the lower side of the leaves.

CONNARACEAE

Rourea rectinervia A. C. Smith, sp. nov. Frutex scandens; ramulis subteretibus fusco-puberulis mox glabrescentibus; foliis (petiolis inclusis) 25–45 cm. longis, 7- vel 9-foliolatis; rhachidibus robustis velut ramulis puberulis, petiolis 5–14 cm. longis basi incrassatis; foliolis coriaceis concoloris suboppositis, paribus 2.5–4.5 cm. distantibus, eis inferioribus minimis, breviter petiolulatis (petiolulis rugosis 4–6 mm. longis), oblongis vel obovato-oblongis, maximis ad 18 cm. longis et 7.5 cm. latis, basi subacutis, apice cuspidatis vel breviter acuminatis, margine integris, supra glabris subtus nervis principali-

bus puberulis, costa crassa supra valde impressa subtus prominentissima, nervis lateralibus 5- vel 6-jugis rectis adscendentibus prope marginem anastomosantibus supra impressis subtus prominentibus, venulis copiose reticulatis subtus leviter elevatis; inflorescentiis 1 vel 2 in axillis foliorum paniculatis, 7-15 cm. longis, ramulis minute fusco-puberulis; calyce maturo puberulo coriaceo subsessili, lobis erectis imbricatis ovatis, circiter 2 mm. longis et 4 mm. latis, rotundatis; capsula curvata 12-14 mm. longa, stylo saepe persistente.

Type, *Krukoff 1660*, collected Dec. 22, 1931, on shore of creek near the source of the Jatuarana River, Machado River region, State of Matto Grosso. The ascending nerves, which are deeply impressed above and prominent beneath, distinguish the species. From *R. frutescens* Aubl., probably its closest ally, the new species is also distinguished by the minutely puberulent rather than griseo-sericeous pubescence.

CAESALPINIACEAE

Tachigalia carinata Gleason, sp. nov. Arbor 12 m. alta, ramulis crassis glabris; stipulae ad bases foliorum et inflorescentiae ramorum atque nodos superiores sine foliis conspicuae persistentes foliaceae, pinnatifidae lobis 3-7, ambitu late ovatae, 10-15 mm. longae, tenuiter canescentes, lobis anguste lanceolatis acuminatissimis, lobo terminali laterales fere aequante; folia paripinnata 7-9-juga; petiolus 3.5-6 cm. longus, crassus, in formicarium leviter dilatatus, supra planus aut subconvexus lateribus carinatis, subtus carinatus vel subrotundatus, glaber; rachis 18-38 cm. longa, minutissime adpressequae puberula, supra plana lateribus carinatis, subtus rotundata vel subcarinata; foliola inter se 25-50 mm. dissita, infima 2 ovata vel ovato-oblonga, 5-12 cm. longa, fere aequilatera, cetera oblongo-lanceolata vel oblonga, 12-18 cm. longa, 4-5.5 cm. lata, basi obtusa vel subrotundata, apice anguste longeque acuminata, utrinque glabra, nervo medio margine inferiori propiore, supra paullum, subtus bene prominente, nervis lateralibus utrinque 7-10 sub angulo 50° orientibus, marginem versus arcuatis et arcuatim connexis, petiolulis atris rugosis 3-4 mm. longis; inflorescentia terminalis vix paniculata, ramis 2-8 elongatis virgatis, rhachide sicut pedicellis hypanthio calyceque arcte canescenti-tomentula, parte inferiore 5 cm. longa sterili; alabastra et flores conferti ad anthesin 2-3 mm. dissiti; bracteae canescentes erectae anguste lanceolatae longissime acuminatae 4 mm. longae, ad anthesin deciduae; pedicelli crassiusculi 3-3.5 mm. longi; hypanthium obconicum paullum obliquum 10-costatum 3-3.5 mm. longum; sepala 5 ad anthesin reflexa apice rotundata, intus canescenti-villosula, exteriora 2 oblonga, 5 mm. longa 3.5 mm. lata, interiora 3 tenuiora 6 mm. longa 5.5 mm. lata; petalum superius obovatum apice rotundatum 7 mm. longum 5 mm. latum, petala 4 lateralibus et inferiora oblonga obtusa 7 mm. longa 3.5 mm. lata, omnia intus prope basin villosa; stamina majora 7 leviter sigmoidea angustissime subulata 11 mm. longa, in parte tertia inferiore ferrugineo-villosa, minora 3 crassiora 9 mm. longa, ceterum

similia; ovarium ad hypanthium excentrice adnatum, stipite villosa 2 mm. longo elevatum, oblongum complanatum 3.5 mm. longum pubescens, stylo gracili 9–10 mm. longo.

Type, *Krukoff 1479*, collected Nov. 28, 1931, on varzea land along river near Tabajara, upper Machado River region, State of Matto Grosso. It is most closely related to *T. formicarium* Harms, from eastern Peru, in which the stipules are somewhat larger, with reduced lateral lobes, the leaflets only 4–6 pairs, the shorter spikes only 5–10 cm. long and ferruginous instead of canescent, and the petals only 4 mm. long and actually shorter than the sepals.

ELIZABETHA PARAENSIS Ducke. Two specimens have been distributed under this name, *Krukoff 1167* and *1184*, both from the upper Cupary River, State of Pará, the first in flower, the second sterile. The leaflets of the sterile specimen are larger, up to 25 mm. long, with veins more conspicuous on both surfaces, the rachis is more pilose, and the leaves are subtended by large protective scales 5 cm. long. The leaflets of the fertile plant are rarely more than 18 mm. long and the scales are replaced by intrapetiolar stipules 5–8 mm. long. Certain individual specimens of *1184*, however, have leaflets scarcely longer than those of *1167*. Ducke noted the variation in size of leaflets also, and it is probable that large leaflets, protective scales, and pubescent habit are characteristic of rapidly growing parts of the plant. Ducke's original description was apparently based on fruiting material bearing young buds. In certain points of floral structure, our specimens differ notably from the original, but the discrepancies can be easily accounted for by further development of the parts. The following addition to the original description is offered:

Bracteae oppositae 20 mm. longae usque medium connatae, parte libera ovata obtusa, apice inflexa vel cucullata; pedicelli 13 mm. longi; hypanthium coriaceum campanulatum, 6.5 mm. longum; sepala 4 mox decidua, ad hypanthium discreta, 16–19 mm. longa, 7–11 mm. lata, ovato-oblonga, paullum falcata, obtusa; petala 5 fere aequalia, anguste oblongo-elliptica, 22 mm. longa, 7–8 mm. lata; stamina fertilia 3, circa 5 cm. longa, sterilia 6, 16–22 mm. longa.

FABACEAE

Diplotropis triloba Gleason, sp. nov. Arbor 30-metralis; rami juniores crassiusculi subteretes minutissime puberuli; petioli 30–45 mm. longi, tenuissime puberuli, rhachis foliorum ultra petiolum 9–11 cm. longa; foliola 9 firma ovali-oblonga 6–8 cm. longa 4–4.5 cm. lata acuta, basi rotundata et paullum obliqua, supra glabra subnitentia, costa impressa, venis venulisque paullum elevatis distincte reticulatis, subtus opaca in sicco brunnescentia minutissime puberula, venis indistinctis; panícula magna floribunda e ramis terminalibus

et in axillis superioribus orientibus composita arcte puberula aut fere velutina, pilis brevibus brunneis, bracteis persistentibus late triangularibus apice incurvis 1 mm. longis; flores in ramis racemosi pedicellis velutinis adscendentibus 4 mm. longis, bracteolis ad basin hypanthii minutis ovatis; hypanthium et calyx falcato-campanulatus velutinus latere posteriore fere 10 mm. longo inferiore brevior; sepala falcato-triangularia acuta 2–3 mm. longa, posteriora quam anteriora paullum longiora; petala omnia libera unguiculata; vexillum 9 mm. longum, supra unguem brevem ad 6 mm. explanatum et fere trilobum, lobis lateralibus triangularibus ad apicem auriculatis, lobo terminali late oblongo rotundato; petala alaria 12 mm. longa, ungui 5 mm. longa, lamina oblonga apice rotundata basi truncata; petala carinalia 12 mm. longa valde inequilatera; stamina 10 alternatim inaequalia 3.5 vel 6 mm. longa, filamentis subulatis glabris; ovarium oblongum 5 mm. longum velutinum; stylum 5 mm. longum apice incurvatum.

Type, *Krukoff 1562*, collected Dec. 7, 1931, on "terra firma" near the source of the Jatuarana River, Machado River region, State of Matto Grosso. An immature pod is 4 cm. long and 8 mm. wide. A second specimen is *Krukoff 1380*, collected near Tabajara, in the upper Machado River region; its leaves are slightly larger and less plainly reticulate above and the pubescence of the inflorescence and calyx is shorter and somewhat sparser. The flower structure is the same. The conspicuously lobed vexillum indicates that the relations of *D. triloba* are with *D. brasiliensis* (Tul.) Benth., which has smaller leaflets prominently reticulate on both sides, a shorter, wider, and less pubescent calyx, and much shorter pedicels.

RUTACEAE

Erythrochiton delitescens Morton, sp. nov. Subg. *Toxosiphon*; frutex erectus; ramuli perspicue rugosi, ca. 25 mm. diametro, glabri, nitidi, internodiis abbreviatis, saepe vix 1 cm. longis; folia solitaria, unifoliolata; petioli usque 7 cm. longi, ca. 1.5 mm. diametro, graciles, glabri, supra evidenter canaliculati, haud teretes, apice articulati; laminae oblanceolatae, maximae 24 cm. longae et 8.7 cm. latae, apice abrupto brevi-acuminatae, basi acuminatae, membranaceae, in statu sicco pallide virides, concolores, integrae, inconspicue glanduloso-punctatae, venis lateralibus primariis (ca. 12) arcuatis et anastomosantibus, intermediis numerosis et prominentibus, venulis copiose reticulatis; pedunculus ut videtur terminalis, usque 11.5 cm. longus, apice furcatus, ca. 6-florus, sulcatus, puberulus, pilis minutis albis, simplicibus, apicem spectantibus, appressis dense obsitus; pedicelli 6–9 mm. longi, apicem versus incrassati, dense puberuli; calyx valvatus, usque ad basin partitus, valde angulatus, lobis 5, lanceolatis, alabastro margine recurvatis, ca. 3 cm. longis, 7 mm. latis, apice longe et gradatim acuminatis, basi paullum angustatis, utrinque dense albido-puberulentis, haud glanduloso-punctatis; corolla ex 5 petalis liberis constata, petalis basi plus minus cohaerentibus, albis, lineari-

spathulatis, ca. 5 cm. longis, usque 6 mm. latis, basi valde angustatis, ca. 3 mm. latis, apice acutis, utrinque dense albido-puberulis, imbricatis; stamina antherifera 2, filamentis brevibus, glabris, antheris linearibus, ca. 9 mm. longis, longitudinaliter dehiscentibus, connectivo magno basi valde dilatato et in auriculis binis producto; stylus ca. 4 mm. longus, basi glaber, sursum dense pubescens; stigmata 5, libera, capitata; gynoecium ex 5 carpellis liberis glabris constatum, ovulis binis ex angulo interiore carpellorum pendulis, superpositis; fructus deest.

Type, *Krukoff 1598*, collected Dec. 21, 1931, in a very old clearing near the source of the Jatuarana River, Machado River region, State of Matto Grosso. Form any years *Erythrochiton Lindenii* (Baill.) Hemsl. of North America was the only known member of the subgenus *Toxosiphon*. In 1905, however, Pilger¹ described *E. trifoliatum* from the Department of Loreto, Peru. Since then one additional species, *E. macropodium* Kraus, has been described. The present species differs from *E. trifoliatum* in its unifoliolate rather than trifoliolate leaves. It differs from *E. macropodium* in its densely puberulent, eglandulose sepals.

Galipea tubiflora A. C. Smith, sp. nov. Frutex 8 m. altus; ramulis teretibus glabris striatis; petiolis teretibus basi incrassatis 3–12 cm. longis; foliis 3-foliolatis, petiolulis 1–2 cm. longis; laminis papyraceis viridibus glabris dense pellucido-punctatis inaequilateralibus (terminali aequilateriali et majore) oblongis, 25–35 cm. longis, 8–11 cm. latis, basi acutis, apice caudato-acuminatis (apice ipso obtuso), margine integris saepe undulatis, pinnatinerviis, costa utrinque prominentissima, nervis lateralibus 10–15 in quoque latere arcuato-ascendentibus prope margines anastomosantibus, utrinque elevatis, venulis copiose reticulatis conspicuis; inflorescentiis axillaribus quam foliis brevioribus, rhachide tereti apicem versus complanata, ramulis brevibus floriferis apice inflorescentiae congestis, juventute luteo-pulverulentis; pedicellis circiter 1 mm. longis; calyce cupuliformi 4 mm. longo minute pulverulento parce glanduloso bevissime dentato; corolla maturitate 3–4 cm. longa, tubo 3 mm. diametro extra glanduloso et minutissime pulverulento intus basi filamentorum albo-villoso, lobis subaequalibus oblongo-lanceolatis, maturitate recurvatis 15 mm. longis et 2.5 mm. latis, apice callosomucronatis; staminibus ut videtur 5 fertilibus, filamentis ligulatis, antheris lineari-oblongis 3–4 mm. longis, basi appendicibus cordatis carnosius 2 mm. longis instructis; disco membranaceo 0.8 mm. longo margine puberulo ovarium cingente; ovario depresso-globoso, loculis plus minusve distinctis ut videtur 1-spermis; stylo glabro corollam subaequante, stigmate incrassato; capsula 5-loculari, carpidiis striatis oblongo-ovoideis circiter 13 mm. longis, dorso obtuse carinatis.

Type, *Krukoff 1538*, collected Dec. 5, 1931, on "terra firma" near

¹ Verh. Bot. Ver. Brandenburg 47: 153. 1905.

Angustura, near the source of the Jatuarana River, Machado River region, State of Matto Grosso. In leaf shape and size, the new species resembles *G. longiflora* Krause, which, however, has a toothed calyx and densely pilose flowers. *G. tubiflora* is probably more closely allied to *G. jasminiflora* (St. Hil.) Engl., from which it differs in its narrower corolla lobes, longer anther connectives, larger leaves, etc. All the flowers of *G. tubiflora* which I have examined have five fertile anthers, whereas the above species have only two.

Esenbeckia coriacea A. C. Smith, sp. nov. Arbor; ramis ramulisque teretibus glabris fuscis vel cinereis rugosissimis copiose lenticellatis; petiolis velut ramulis, 2–4 cm. longis; foliis 2- vel 3-foliolatis, petiolulis incrassatis circiter 2 mm. longis cum petiolis articulatis, laminis coriaceis glabris pellucido-punctatis inaequilateralibus (praeter terminales) oblongis, 12–20 cm. longis, 5–8 cm. latis, basi acutis, apice breviter acuminatis (apice ipso obtuso), margine integris et leviter recurvatis, pinnatinerviis, costa crassa supra leviter elevata subtus prominentissima, nervis lateralibus circiter 12-jugis patulis, prope margines adscendentibus et anastomosantibus, utrinque elevatis, venulis anastomosantibus subtus conspicuis; inflorescentiis terminalibus paniculatis, ramis juventute puberulis, bracteolis deciduis coriaceis acutis 1–2 mm. longis subtentis; floribus utrinque dense pallide puberulis; pedicellis 1.5–3 mm. longis prope basin minute bibracteolatis; calyce 5-lobato, lobis deltoideis obtusis, circiter 0.8 mm. longis et 1.2 mm. latis; petalis 5 albis carnosis ovato-oblongis, circiter 3.7 mm. longis et 2 mm. latis, basi angustis, apice acutis; staminibus 5 glabris, filamentis carnosis circiter 2 mm. longis, distaliter contractis, antheris dorsifixis versatilibus ovoideis, circiter 0.8 mm. longis, basi subcordatis, apice apiculatis; disco 10-lobato, dense carnosio-tuberculato; stylo carnosio circiter 0.8 mm. longo, stigmate 5-lobato; fructu glabro, maturitate 3 mm. longo et 4 mm. diametro, rugosissimo, loculis 1-spermis.

Type, *Krukoff 1667*, collected Dec. 23, 1931, on "terra firma" near the source of the Jatuarana River, Machado River region, State of Matto Grosso. Other collections are: *Rusby 2617, 2663*, both from the Falls of the Madeira River, State of Amazonas. It is a species related to the Andean *E. alata* (Karst. & Tr.) Tr. & Pl., compared with which it has the leaf-blades more coriaceous, the calyx-lobes shorter, and the mature fruit larger and more conspicuously rugose.

Zanthoxylum Krukovii A. C. Smith, sp. nov. Arbor ad 30 m. alta, trunco 1 m. diametro; ramulis subteretibus rugosissimis glabris fuscis, prope apices 4–6 mm. diametro; foliis adscendentibus 15–30 cm. longis, petiolis rhachidibusque purpurascentibus striatis juventute cinereo-puberulis, petiolis 3–6 cm. longis basi incrassatis et semiteretibus, rhachidibus teretibus, internodiis 1–3 cm. longis; foliolis 4–7-jugis, petiolulis gracilibus rugosis puberulis 4–6 mm. longis, laminis subcoriaceis praeter nervos subtus glabris dense et conspicue

pellucido-punctatis oblongis vel ovato-oblongis, 6–9 cm. longis (eis basis brevioribus), 2.5–3.5 cm. latis, basi inaequilateraliter cuneatis, apice breviter et obtuse acuminatis, margine integerrimis, costa supra impressa subtus prominente, nervis lateralibus primariis 8–12 in quoque latere patulis prope margines anastomosantibus utrinque elevatis, venulis copiose reticulatis elevatis; inflorescentiis terminalibus paniculatis ad 20 cm. longis et latis multifloris, ramulis teretibus striatis puberulis, bracteis minutis deciduis subtentis, ramulis extimis brevibus; floribus ♂ in glomerulis 3–5-floris congestis sessilibus, basi 3 vel 4 bracteis ovatis 0.6 mm. longis margine minute fimbriatis circumdatis; calycis lobis 5 imbricatis ovato-deltaideis circiter 0.7 mm. longis et latis; petalis 5 anguste imbricatis submembranaceis albis ovatis, circiter 1.5 mm. longis et 0.9 mm. latis, apice subacutis; staminibus 5 corollam subaequantibus, filamentis teretibus, antheris ovoideis cordatis 0.7 mm. longis; ovarii rudimento breviter conico sulcato stigmatibus 3 sessilibus coronato.

Type, *Krukoff 1587*, collected Dec. 20, 1931, on "terra firma" near the source of the Jatuarana River, Machado River region, State of Matto Grosso. It is a species related to *Z. cuiabense* Engl., than which it has more numerous, narrower, and more conspicuously punctate leaflets. *Z. Krukovii* has the flowers absolutely sessile, the stamens equaling rather than exceeding the petals, and the rudimentary ovary 3- rather than 2-parted.

MELIACEAE

Trichilia punctata A. C. Smith, sp. nov. Frutex; ramulis elongatis teretibus striatis glabris copiose lenticellatis; foliis alternis 25–45 cm. longis, petiolis decidue pilosis, 4–7 cm. longis, canaliculatis bialatis, rhachidibus leviter canaliculatis striatis, foliolis plerumque 9 suboppositis, petiolulis rugosissimis 4–5 mm. longis (foliolae terminalis 5–15 mm. longis), laminis coriaceis fuscis dense pellucido-punctatis oblongis, 8–17 cm. longis, 3–6 cm. latis, basi subattenuatis, apice cuspidatis, margine subintegris et leviter recurvatis, utrinque glabris, pinnatinerviis, nervis lateralibus 13–15-jugis patulis prope margines adscendentibus, cum costa supra leviter impressis subtus prominentibus, venulis copiose reticulatis; paniculis axillaribus quam petiolis brevioribus e basi 2- vel 3-fidis, ramulis dense cinereo-pilosis; floribus sessilibus, bracteis pilosis deltaideis 1 mm. longis subtentis; calyce 5-dentato, dentibus deltaideis acutis 0.7 mm. longis parvis puberulis; petalis 5 haud imbricatis oblongis obtusis, 3.3–4 mm. longis, circiter 1.8 mm. latis; staminibus 10–12, in fructu saepe persistentibus; filamentis fere ad medium connatis, circiter 1.6 mm. longis, superne pilosis; antheris obtusis, circiter 0.5 mm. longis, pilis 0.3 mm. longis dense hirsutis; ovario sessili conico sub anthesi 1.5–2 mm. longo, dense adpresso-albo-hirsuto, 3-loculari, loculis 1-spermis; stigmatibus subsessilibus (stylo ad 0.3 mm. longo), discoideo; capsulis ovoideis vel trigonis, maturitate ad 25 mm. longis et 10 mm. diametro, minute velutinis, 3-spermis, seminibus collateralibus arillo vestitis.

Type, *Krukoff 1437*, collected Nov. 24, 1931, on varzea land near shore of river near Tabajara, upper Machado River region, State of Matto Grosso. It is a species of the section *Eutrichilia*, allied to *T. guianensis* Kl., compared with which it has the inflorescence more compact and fewer flowered, and the stigma subsessile (*T. guianensis* has a noticeable style). In foliage, our species has the leaves 4-jugate rather than 3-jugate, the leaflets more coriaceous and pellucid-punctate, and the nerves impressed rather than plane above.

Trichilia Krukovii A. C. Smith, sp. nov. Arbor circiter 13 m. alta, trunco prope basin 0.5 m. diametro; ramis ramulisque subteretibus rugosis juventute arcte fusco-puberulis; foliis ad 60 cm. longis, petiolis velut ramulis decidue puberulis, 8–10 cm. longis, crassis (3–5 mm. diametro), inferne 2-alatis, rhachidibus teretibus, foliolis 7 vel 9 suboppositis, petiolulis rugosis incrassatis 3–5 mm. longis (foliolae terminalis ad 30 mm. longis), laminis coriaceis oblongis, 12–23 cm. longis, 3.5–8 cm. latis, basi acutis vel cuneatis, apice cuspidatis vel breviter acuminatis, margine crenulatis et recurvatis, supra fuscis et praeter costam puberulam glabris, subtus pallidis minute puberulis mox glabris, pinnatinerviis, nervis lateralibus 14–22-jugis rectis patulis prope margines adscendentibus, cum costa supra planis subtus prominentibus, venulis copiose reticulatis; paniculis multifloris axillaribus quam foliis brevioribus (ad 20 cm. longis et 10 cm. latis), ramulis angulatis striatis dense cinereo-puberulis; floribus pedunculis brevibus subsessilibus, extra subtilissime argenteo-puberulis demum glabrescentibus: calyce 5-lobato, lobis late ovatis, 1.5 mm. longis, 1.8 mm. latis, basi angustioribus; petalis 5 aestivatione quincuncialibus oblongis, circiter 3.7 mm. longis et 2 mm. latis, apice obtusis; filamentis connatis, tubo stramineo utrinque puberulo 1.5 mm. longo, margine inter antheras dentes lanceolatos 0.8 mm. longos gerente; antheris 10 subacutis 1.2 mm. longis; ovario sessili subgloboso sub anthesi circiter 2 mm. diametro, dense et arcte albo-hirsuto, 3-loculari, loculis 1-spermis; stylo carnoso 0.5 mm. longo apice incrassato 3-denticulato.

Type, *Krukoff 1021*, collected Sept. 5, 1931, on "terra firma" at Fordlandia, Tapajos River region, State of Pará. It is a species of the section *Moschoxylum*, related to *T. septentrionalis* C. DC., from which it differs by its thicker leaves, smaller panicles, larger flowers, and hirsute rather than glabrous ovaries.

Cabralea erismatica A. C. Smith, sp. nov. Arbor ad 30 m. alta, prope basin 0.5–1 m. diametro; ramulis subteretibus glabris fuscis; foliis glabris alternis 50–80 cm. longis, petiolis rhachidibusque subteretibus, petiolis basi incrassatis, foliolis plerumque 9–11-jugis suboppositis, petiolulis rugosis 4–7 mm. longis, laminis papyraceis viridibus epunctatis falcato-oblongis, 12–19 cm. longis (eis basis paullo brevioribus), 3.5–5.5 cm. latis, basi inaequilateraliter cuneatis, apice longe acuminatis, margine integris vel undulatis, costa leviter

curvata utrinque prominente, nervis lateralibus primariis 10–15 in quoque latere patulis prope margines adscendentibus utrinque leviter elevatis, venulis reticulatis subplanis; paniculis axillaribus quam foliis brevioribus (15–35 cm. longis) pedunculatis multifloris, ramulis striatis, ultimis breviter cinereo-strigosis; floribus pedicellatis (pedicellis ad 3 mm. longis), bracteis pilosis minutis subtentis; sepalis 5 imbricatis late ovatis rotundatis circiter 2 mm. longis et 2–3 mm. latis, extra puberulis, margine membranaceis et fimbriatis; petalis 5 haud imbricatis submembranaceis parce puberulis oblongis obtusis, 7–8 mm. longis, circiter 3 mm. latis; filamentis connatis, tubo carnosio glabro cylindrico circiter 6 mm. longo, apice crenato, antheris oblongis obtusis 1 mm. longis, dorso prope basin sessilibus; disco carnosio tubuloso erecto 2 mm. longo, extra glabro, intus dense strigoso, apice incrassato et crenato; ovario sessili arcte strigoso conico sub anthesi 1.5–2 mm. longo, 5-loculari, loculis 2-ovulatis; stylo crasso 5 mm. longo basi puberulo, stigmatе carnosio discoideo 1 mm. diametro.

Type, *Krukoff 1115*, collected Sept. 14, 1931, in high forest in the region of the upper Cupary River, on the plateau between the Xingu and Tapajos Rivers, State of Pará. Another collection from the same region is *Krukoff 1121*. It is said to be a large tree with conspicuous buttresses; the outer bark of the trunk is thick and ashy-gray, the inner bark being reddish-brown. It is locally known as "Cedrahy." It is probably most nearly allied to *C. laevis* C. DC., which has considerably smaller leaves and leaflets, but of which the flowers are undescribed. No species of *Cabrlea* have previously been described from this part of the Amazon basin, the genus being best developed farther south.

MALPIGHIACEAE

ALCOCERATOTHRIX. Niedenzu separated the genus *Alcoceratothrix* from *Byrsonima* chiefly because of the structure of the hairs, which in the segregate are wholly or partially branched and "alcis cornua imitantes." We are scarcely disposed to agree with a generic segregation on such grounds, but distribute the material under Niedenzu's name to conform with the usage in his recent monograph of the family. Of the two species, *A. stipulacea* has trimorphic hairs and non-glandular sepals, while *A. rugosa* is stated to have one form of hairs only and glandular sepals.

In *Krukoff 1555* the sepals are non-glandular and the hairs trimorphic; it has been referred accordingly to *A. stipulacea*. In comparison with *Martius 567* cited by Niedenzu, its leaves are less pubescent on both sides, the upper internodes velutinous rather than hirsute, and the persistent stipules only 9–10 mm. long.

In *Krukoff 1360* the sepals are glandular and the whole habit is that of the well known *A. rugosa*, represented in our herbarium by numerous

specimens from Guiana. While Niedenzu states that the hairs are only a fourth of a millimeter long, in almost all of our specimens, including some cited by Niedenzu, they surpass a millimeter and even reach 3 mm. on the stipules, while the elk-horn hairs are distributed chiefly on the lower side of the leaves and in the inflorescence. *Krukoff 1360* has such hairs limited to the inflorescence and sepals, and bears on the lower side of the leaf simple vertical hairs 1 to 15 mm. long.

VOCHYSIACEAE

Erisma parvifolium Gleason, sp. nov. Arbor excelsa ad 30 m. alta, ramulis teretibus, cortice cinereo tenui mox exfoliato et brunnescente, ramulis novellis gracilibus 4-sulcatis fuscis tenuiter stellato-tomentellis, internodiis 15–50 mm. longis; folia opposita vel verticillata; petioli crassi 3–6 mm. longi, ut ramulis utrinque tomentelli et supra breviter brunneo-pilosi; laminae subcoriaceae anguste oblongae 8–13 cm. longae 2.5–5.5 cm. latae, in apiculam brevem abrupte acuminatae, margine integro paullum (tantum in sicco) revolutae, basi obtusae vel rotundatae, supra pallide virides subnitentes, subtus fuscae tenuissime stellato-pubescentes et ad venas venulasque parce pilosae; costa supra impressa; venae secundariae supra leviter impressae subtus elevatae, rectiusculae, prope marginem arcuatim conjunctae, venulis inconspicuis utrinque tenuissime reticulatis elevatisque; panícula ampla ramosa terminalis, 1–2 cm. longa tenuiter stellato-pubescent, cincinnis 3–5 floris rectiusculis vel leviter flexuosis; bracteae majores foliaceae oblique rotundato-ovatae 7–8 mm. longae 6–6.5 mm. latae sessiles minute stellato-pubescentes, obscure venosae; bracteae minores oblanceolatae 4–5 mm. longae, 1.5 mm. latae, acutae vel acuminatae, ad basin cuneatae, molliter pubescentes; flores solitarii in axilla cujusque bracteae minoris, pedicello 3 mm. longo; sepala basi connata oblonga, parte libera sepalis primi et quinti 2.5 mm. longa acuta, secundi et tertii 3.5–4 mm. longa obtusa, omnia subcarnosa molliter stellato-pubescentia; sepalum quartum petaloideum rotundatum 9 mm. longum, ad basin purpureo-pilosum, infra basin in calcar anguste subulatum ab ovario pedicelloque liberum 5–6 mm. longum angustatum, post anthesin deciduum, basi persistente poculi-formi; petalum unicum triangulari-obovatum 18 mm. longum, basi cuneatum, superne bilobum, lobis obtusis 4 mm. longis; stamen unicum, filamento gracili 6.5 mm. longo, anthera lanceolata extrorsa 2.8 mm. longa, dorso affixa; ovarium inferum, ovulis 2, stylo subulato 6 mm. longo, post anthesin paullum supra basin deciduo, stigmatibus ovoideo capitato 0.5 mm. longo; pedicelli fructiferi leviter incrassati 5 mm. longi; sepala post anthesin accrescentia et cum ovario samaram formantia, sepalum quarto breviter calcarato incurvato puberulo 3 mm. longo, ceteris chartaceis reticulato-venosis utrinque minutissime stellato-puberulis, primo recto 10 mm. longo, secundo oblongo inequilatero 20 mm. longo, tertio oblongo leviter falcato 60 mm. longo, quinto falcato-ovato 8 mm. longo; nux glabra compressa 1 cm. longa tota longitudine ad calycem adnata; stylus persistens 4 mm. longus.

Type, *Krukoff 1401* (with flowers and immature fruit), collected Nov. 23, 1931, on "terra firma" near Tabajara, upper Machado River region, State of Matto Grosso. *Krukoff 1332*, collected at the same place, is identical. *Krukoff 1679*, collected at the source of the Jatuarana River, Machado River region, is in fruit; its leaves are notably smaller, measuring 5–10 cm. long and 18–32 mm. wide. In all details of pubescence and venation it agrees with the flowering specimens, and the upper leaves of the latter are also similar in their dimensions.

Although most of the ten described species of *Erisma* are rather poorly known, the foliar characters alone are sufficient to separate our species, which is distinct in its narrow leaves pubescent on the lower surface. It clearly stands nearest to *E. uncinatum* Warm., which has much longer petioles, longer and proportionately wider leaf-blades cuneate to the base, smaller bracts, very short pedicels, smaller flowers, acuminate sepals, and a large hooked spur.

Erisma petiolatum Gleason, sp. nov. Arbor ad 25 m. alta; ramuli juveniles tenuissime ferrugineo-tomentelli, inter nodos leviter compressi, mox teretes, glabri, et purpurascens; folia opposita; petioli crassissimi tomentelli 2–2.5 cm. longi, supra alte canaliculati, ad lateres argute angulati; laminae subcoriaceae, elliptico-oblongae, 20–28 cm. longae, 7–10 cm. latae, ad apicem rotundatam et in apiculam acuminatam 1–2 cm. longam productae, infra medium ad basin rotundatam sensim angustatae, supra glabrae, subtus minutissime stellato-puberulae, costa supra impressa, subtus prominente, venis secundariis supra obscuris, subtus elevatis rectis, imum ad marginem arcuatim connexis; venulis utrinque arctissime reticulatis; panicula 2 dm. longa, ferruginea, divaricato-ramosa; cincinni oppositi et ad apicem aggregati, 2–5 mm. pedunculati, circa 5-flori, jam immaturi; bractae majores rotundato-ovatae, paullum inequilaterae, 6–7 mm. longae, 4–4.5 mm. latae, tenuissime pubescentes; bractae minores lineari-subulatae, 1 mm. longae; pedicelli 1.5 mm. longi; sepala more generis inaequales, calcare crasso obtuso erecto, in alabastro 1.6 mm. longo.

Type, *Krukoff 1334*, collected Nov. 12, 1931, on "terra firma" near Tabajara, upper Machado River region, State of Matto Grosso. *Krukoff 1376*, from the same place, differs only in a slightly less developed acumen on the leaves. Notwithstanding the lack of mature flowers and fruit, and the risk of burdening literature with a synonym, I feel confident that these specimens represent an unrecognized species. The last treatment of the genus, by Warming, is nearly fifty years old, and only one species has been described since then. Warming distinguished two sections, the first with the lower bracts much larger than and concealing the upper, the second with bracts more nearly uniform in size. While our species belongs

to the second group, foliar differences also exist which separate it from the two known species of the first. In the second group, *E. Japura* has the spur adnate to the ovary and pedicel and the leaves are retuse; *E. calcaratum* has a pendent spur, small leaves, short petioles, and poorly developed marginal vein; *E. uncinatum* differs in the size and shape of its leaves and notably in the peculiar shape of its spur; *E. nitidum* has about half as many secondary veins which are arcuately joined far inside the margin and the petioles are much shorter; *E. micranthum* has much smaller leaves without a connecting marginal vein and a deflexed spur. In *E. fuscum* Ducke, recently described, the leaves are short-petioled, broadly obovate, and glabrous.

EUPHORBIACEAE

Sapium leitera Gleason, sp. nov. Arbor 8 m. alta glabra; ramuli graciles tenuiter striati ad apicem nodorum lenticellis ellipticis ornati; folia irregulariter alterna vel subopposita; stipulae parvae coriaceae ovatae mox deciduae; petioli graciles 3–4 cm. longi striati apicem versus glandula una rugosa notati; laminae chartaceae late ellipticae 9–14 cm. longae, 6–8 cm. latae, apice rotundatae vel paullo emarginatae, margine anguste cartilagineo incrassatae, infime late rotundatae ad basin cordatam, venis lateralibus utrinsecus circa 16, sub angulo 70° orientibus, arcuato-adscententibus et prope marginem curvatis, supra distinctis planis, subtus elevatis, venis secundariis utrinque reticulatis; spicae terminales in fructu 5 cm. longae; capsulae stipite crasso pyramidato angulato 2 mm. longo insidentes, late obovoideae vel pyriformes, basi angustatae, 18 mm. longae glabrae 6-angulatae, stylo deciduo, parietibus crasse crustaceis; semina 3, obovoidea, 5.5 mm. longa, a hilo quadrangulari ad summum columellae affixa, pseudo-arillo brunneo rugoso oblecta.

Type, *Krukoff 1656*, collected Dec. 22, 1931, on "terra firma," near the source of the Jatuarana River, Machado River region, State of Matto Grosso. A vernacular name is "Burra leitera." The specimen is apparently identical with flowering specimens collected by Steinbach in Bolivia and distributed under the name *Sapium peloto* Pax & Hoffm.

HIPPOCRATEACEAE

Salacia mauritioides A. C. Smith, sp. nov. Frutex scandens glaber; ramis ramisque teretibus cinereis vel fuscis; petiolis crassis rugosis canaliculatis 15–25 mm. longis; laminis coriaceis olivaceis oblongis, 16–25 cm. longis, 6–12 cm. latis, basi obtusis vel cuneatis, apice acutis, margine integris et leviter recurvatis, utrinque parcissime nigro-punctatis ac etiam subtus squamas luteas minutas densius gerentibus, costa utrinque prominentissima, nervis lateralibus primariis 7–10 in quoque latere arcuato-adscententibus prope margines anastomosantibus utrinque elevatis, venulis anastomosantibus plus minusve immersis; cymis axillaribus ad 3 cm. longis et latis, supra basin divisis, ramis dichotome ramulosis angulatis bracteatis, bracteis suboppositis del-

toideis minutis; floribus subsessilibus (pedicellis ad 0.5 mm. longis), ubique minutissime ferrugineo-puberulis, maturitate 2.5 mm. diametro; sepalis parvis deltoideis subacutis, 0.5 mm. longis, 0.8 mm. latis, margine eroso-ciliatis; petalis tenuiter carnosis obovato-oblongis, 1.5 mm. longis, 1 mm. latis, margine eroso-fimbriatis; disco breviter tubuloso erecto, 0.4 mm. longo, margine integro; staminibus 3 erectis, filamentis gracilibus 0.8 mm. longis, antheris transverse reniformibus 0.4 mm. latis, rima transversa dehiscentibus; ovario 3-lobato 3-loculari, ovulis in quoque loculo 2 superpositis axi affixis; stylo brevi crasso (0.2 mm. longo), stigmatibus 3-lobato, lobis oblongis recurvatis bilobis, staminibus alternis; drupis ovoideis, maturitate 3–4 cm. longis et 2–2.5 cm. latis, pericarpio lignoso 4 mm. crasso, extra rugosissimo, 3-locularibus (loculo 1 interdum obsoleto), dissepimentis coriaceis; semine in quoque loculo solitario nigrescente.

Type, *Krukoff 1454*, collected Nov. 25, 1931, on varzea land along a creek near Tabajara, upper Machado River region, State of Matto Grosso. The plant is locally known as "Goapeua." It is a species of the Section *Tontelea* Miers, in which it is related to *S. Miersii* Peyr. and *S. corymbosa* Huber. From both of these species, *S. mauritioides* is distinguished by its larger leaves of more coriaceous texture and its slightly smaller flowers. The fruit of the new species is very characteristic, bearing a superficial resemblance, in size and texture of pericarp, to the fruit of the palm *Mauritia flexuosa* L. f. The fruit of the two allied species above mentioned is not known. *S. Miersii* was placed by Miers¹ in the genus *Clercia* (*C. micrantha*), but since the distinction between *Clercia* and *Tontelea* is based upon fruit characters, it is likely that Peyritsch's treatment of the species² is correct.

(to be concluded)

¹ Trans. Linn. Soc. 28: 379. 1872.

² Mart. Fl. Bras. 11. 1: 147. 1878.

INDEX TO AMERICAN BOTANICAL LITERATURE

1930-1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Plantae Krukovianae

H. A. GLEASON AND A. C. SMITH

(concluded from page 365)

STERCULIACEAE

Sterculia megalocarpa A. C. Smith, sp. nov. Arbor ad 25 m. alta, trunco circiter 1 m. diametro; ramulis crassis cinereis striatis, juventute ferrugineo-pilosis mox glabris; stipulis subcoriaceis glabrescentibus lanceolatis 10–17 mm. longis; foliis ad apices ramulorum congestis; petiolis semiteretibus striatis 2.5–6 (rare ad 8) cm. longis, basi apiceque incrassatis, pilis adpressis ferrugineis strigosis; foliis integris coriaceis opacis oblongis vel ovato-oblongis, 12–21 cm. longis, 6–11 cm. latis, basi rotundatis saepe subcordatis, apice cuspidatis vel breviter acuminatis, margine integris undulatis, supra glabris, subtus densissime et arcte ferrugineo-tomentosis (pilis stellatis 4-ramosis 0.2–0.3 mm. latis), pinnatinerviis (e basi 5- vel 7-nerviis), nervis lateralibus 10–12 in quoque latere rectis adscendentibus prope margines anastomosantibus, cum costa supra elevatis subtus prominentibus, venulis reticulatis supra planis subtus elevatis; inflorescentiis desideratis; carpidiis vetustis maximis oblongo-ovoideis falcatis, 15–20 cm. longis, 9–12 cm. latis, juventute arcte ferrugineo-tomentosis, maturitate glabris, breviter stipitatis, pericarpio fibroso sutura 2.5–4.5 cm. crasso (Pl. 21, f. 1).

Type, *Krukoff 1675*, collected Dec. 27, 1931, on “terra firma” near the source of the Jatuarana River, Machado River region, State of Matto Grosso. The plant is locally known as “Achicha.” It is a species distinguished from other South American *Sterculiae* by its extraordinarily large fruit, which is comparable only to the fruit of *S. Chicha* St. Hil., which, however, has lobed leaves. *S. megalocarpa* is allied to *S. pruriens* (Aubl.) Schum., *S. pilosa* Ducke, and *S. Tessmannii* Mildbr. From *S. pruriens* the present species differs by its pubescent leaves, from *S. pilosa* by its short-acuminate leaves. *S. Tessmannii* is said to have longer petioles, longer-acuminate leaves, and fewer lateral nerves than our species. The fruits of the first two of these species are known to be much smaller than ours; of *S. Tessmannii* the fruit is not yet known.

GUTTIFERAE

Calophyllum angulare A. C. Smith, sp. nov. Arbor ad 30 m. alta, trunco 1 m. diametro; ramulis crassis fuscis, juventute quadrangularibus et fusco-vel cinereo-puberulis, internodiis 1–2 cm. longis; petiolis saepe nigrescentibus rugosis leviter canaliculatis glabris 13–20 mm. longis; laminis rigide coriaceis

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glabris oblongis vel ovato-oblongis, 8–11 cm. longis, 3.5–5.5 cm. latis, basi acutis vel cuneatis, apice breviter acuminatis, margine integris incrassatis, costa supra saepe impressa subtus prominentissima et striata, nervis laterilibus numerosissimis densissimis parallelis; inflorescentiis axillaribus racemosis vel e cymis brevibus compositis, 2–5 cm. longis, 6–15-floris, ubique dense ferrugineo-puberulis; bracteolis ovatis 4–6 mm. longis mox deciduis; pedicellis 2–5 mm. longis; sepalis 4 intus glabris ovatis, 5–6 mm. longis, 3 mm. latis; petalis plerumque nullis interdum 2, sepalis similibus sed glabris et membranaceis; staminibus numerosis, filamentis gracilibus circiter 2.5 mm. longis, antheris 1 mm. longis; ovario glabro ovoideo sub anthesi 1.5 mm. longo, stylo quam ovario brevior, stigmate truncato.

Type, *Krukoff 1442*, collected Nov. 25, 1931, on varzea land near river-shore, near Tabajara, upper Machado River region, State of Matto Grosso. The collector notes that the local name is "Jacareuba." The flowers are white, and the inner bark yields a yellow latex. "Jacareuba" is also applied to the other species of the genus, notably *C. brasiliense* Camb., from which the present species differs in aspect of inflorescence. It is more closely allied to *C. pachyphyllum* Pl. & Tr., with which it has in common a ferruginous-puberulous tomentum on the inflorescence, a character which distinguishes these two species from others in South America. The present species differs from *C. pachyphyllum* by the slightly smaller leaves which are short-acuminate rather than obtuse or emarginate at apex, the longer inflorescence with more numerous flowers, and the lack of petals. *C. pachyphyllum*, which is represented by *Krukoff 1495* from the same region as the new species, usually has 4 petals; *C. angulare* is usually apetalous, rarely with 2 petals.

CARYOCARACEAE

Caryocar dentatum Gleason, sp. nov. Arbor 20 m. alta; ramuli subteretes crassi, 4 dm. infra apicem 5 mm. diametro fistulosi, tenuiter brunneo-pubescentes, internodiis 35–45 mm. longis; petioli inferiores 65 mm. superiores 25 mm. longi puberuli, stipellis 1–3 subulatis curvatis 3 mm. longis ornati; petioli puberuli 4–7 mm. longi inter se subaequales; laminae firmulae anguste oblongae vel ellipticae, in quoque folio fere aequales, majores ad 120 mm. longae 45 mm. latae, juniores minores, basi obtusae vel late cuneatae, apice breviter acuminatae, margine grosse dentatae, dentibus triangularibus obtusis sursum vergentibus saepissime 5–8 mm. inter se distantibus et 2–3 mm. altis, venis venulisque supra paullum impressis subtus elevatis, tenuissime et pulcherrime reticulatis, secundariis in $\frac{3}{4}$ longitudinis subrectis prope marginem arcuato-conjunctis, pagina superiore ad venam mediam minutissime puberula ceterum glabra, inferiore puberula ad venas et venulas majores; pedunculus crassus puberulus 35 mm. longus; racemus 4 cm. longus circa 20-florus,

rhachide pedicellis et calycibus velutino-tomentellis; pedicelli adscendentes ad 15 mm. longi, prophyllis mox delapsis prope basin sitis; calyx late hemisphaericus in alabastro maturo 7 mm. latus, basi in pedicellum crassum 2 mm. longum decurrens, lobis 5 late triangulari-ovatis 2 mm. longis 3 mm. latis obtusis; petala oblongo-elliptica 25 mm. longa 9 mm. lata obtusa; stamina numerosa (usque 100?), filamentis 6 cm. longis carmesinis; fructus ignotus; nuces subglobosae 6 cm. longae 5 cm. latae densissime spinosae aculeis 15 mm. longis.

Type, *Krukoff 1294*, collected Nov. 7, 1931, on "terra firma" near Calama, Madeira River region, State of Amazonas. While a few other species of *Caryocar* have similarly narrow leaves, in none of them are they so deeply dentate. This feature together with the tomentose pedicels and calyx, the pubescent petiole, and the nearly basal prophylls serves to separate *C. dentatum* from all other described species of the genus.

LECYTHIDACEAE

Lecythis jarana (Huber) A. C. Smith, comb. nov. *Chytroma jarana* Huber, Bol. Mus. Goeldi 6: 209. 1910, nomen. *Holopyxidium jarana* Ducke, Arch. Jard. Bot. Rio 4: 152. 1925. *Eschweilera jarana* Ducke, Arch. Jard. Bot. Rio 5: 177. 1930.

Lecythis jarana* var. *latifolia (Ducke) A. C. Smith, comb. nov. *Eschweilera jarana* var. *latifolia* Ducke, Arch. Jard. Bot. Rio 5: 178. 1930.

Pará: upper Cupary River, plateau between Xingu and Tapajos Rivers, *Krukoff 1213*. Mr. Krukoff notes his plant as a tree 30 meters high and with a trunk slightly more than 1 meter in diameter, with the local name of "Jarana." Study of the flowers makes necessary the above new combination. The vertex of the ovary is more or less flat, bearing in the center a style about 2 mm. long; the 4-celled ovary has a central column, upon which the several ovules are borne on distinct funicles. These characters are those of *Lecythis* rather than of *Eschweilera* (sect. *Chytroma*). In addition, the general aspect of the plant, of which the comparatively thin leaves do not resemble those of *Eschweilera*, is that of *Lecythis*. Fruits such as those described and figured by Ducke¹ are certainly of *Lecythis* rather than *Eschweilera*. These fruits were probably taken from *L. jarana* var. *latifolia* rather than from *Eschweilera retusa* (Berg) Nied., as implied by Ducke in his second publication² discussing this alliance.

Eschweilera* (*Eueschweilera*) *polyantha A. C. Smith, sp. nov. Arbor 20 m. alta, trunco ad 1 m. diametro; ramulis cinereis vel fuscis teretibus parce lenticellatis; petiolis rugosis leviter canaliculatis 8–10 mm. longis; laminis

¹ Arch. Jard. Bot. Rio 4: 152. pl. 15 (as *Holopyxidium retusum*). 1925.

² Arch. Jard. Bot. Rio 5: 178. 1930.

coriaceis olivaceis glabris oblongis, 12–17 cm. longis, 4–7 cm. latis, basi obtusis vel cuneatis, apice caudato-acuminatis, margine obsolete serrulatis, pinnatinerviis, costa valida, nervis lateralibus primariis 8–10 in quoque latere arcuato-adscententibus prope margines anastomosantibus, utrinque elevatis, venulis copiose reticulatis supra leviter elevatis subtus prominulis; paniculis terminalibus et axillaribus (1–4 in axillis) ramosissimis 2–8 cm. longis multifloris; rhachidibus et ramulis subteretibus dense fusco-puberulis; pedicellis teretibus 2.5–3.5 mm. longis velut rhachidibus puberulis; sepalis carnosius minute puberulis oblongis, circiter 3 mm. longis et 1.5 mm. latis, apice obtusis, margine parce glandulosis; petalis submembranaceis glabris luteis ovatis, 7–9 mm. longis, 5–6 mm. latis, apice rotundatis; androphoro explanato 8–10 mm. longo, ligula 2 mm. lata basi dilatata, galea subsphaerica 4–5 mm. diametro, fimbriata et subtus densissime echinata, appendiculis anantheris imbricatis linearibus 2.5–3.5 mm. longis obiecta; staminibus circa annulum et in ligula prope basin numerosis (60–120), filamentis gracilibus 0.5–0.8 mm. longis apice angustis, antheris subglobosis circiter 0.4 mm. diametro; ovario semisupero, vertice depresso-conico rugoso umbonato, loculis 2, ovulis in quoque loculo 4 vel 5 erectis e basi sessilibus.

Type, *Krukoff 1318*, collected Nov. 12, 1931, on “terra firma” near Tabajara, upper Machado River region, State of Matto Grosso. The local name is “Ripeiro,” a name which is apparently not used for other Lecythidaceae in the region. It is allied to several small-flowered species from Guiana, *E. parviflora* (Aubl.) Miers, *E. micrantha* (Berg) Miers, and *E. Sagotiana* Miers. From these species *E. polyantha* differs by its copiously branched many-flowered inflorescences, and by the less conspicuous venation on the lower surface of leaves.

Eschweilera (*Jugastrum*) **truncata** A. C. Smith, sp. nov. Arbor glaberrima 15–20 m. alta; ramis ramulisque cinereis teretibus striatis lenticellatis; petiolis crassis rugosis canaliculatis 12–20 mm. longis; laminis coriaceis olivaceis opacis oblongis, 15–40 cm. longis, 5–12 cm. latis, basi obtusis vel cuneatis, apice acuminatis (acumine ad 2 cm. longo), margine leviter recurvatis et integris vel obsolete serrulatis, subtus parce nigro-punctatis, pinnatinerviis, costa crassa utrinque prominentissima, nervis lateralibus primariis 10–18 in quoque latere prope margines anastomosantibus, supra elevatis subtus prominentibus, venulis copiosissime reticulatis utrinque elevatis; paniculis plerumque terminalibus ramosis 5–16 cm. longis; rhachidibus fuscis angulatis rugosis lenticellatis, geniculis incrassatis; pedicellis crassis 8–10 mm. longis; sepalis subaequalibus carnosius laevibus ovato-oblongis, 5–7 mm. longis, 4.5–5.5 mm. latis, apice rotundatis, margine membranaceis; petalis tenuiter carnosius ovatis, 8–17 mm. longis, 6–13 mm. latis, apice rotundatis; androphoro explanato 20–25 mm. longo, ligula 5–8 mm. lata, galea carnosa 7–10 mm. diametro, margine fimbriata et subtus dense echinata, appendiculis anantheris imbricatis

oblongo-linearibus 2–4 mm. longis obiecta, staminibus circa annulum numerosissimis, filamentis carnosis circiter 1.5 mm. longis apice angustis, antheris oblongo-ovoideis 0.5 mm. longis; ovario subsupero, vertice conico laevi, stylo brevi obtuso, loculis 2, ovulis in quoque loculo 6–10 angulatis erectis e basi sessilibus; pyxidio subgloboso basi truncato apice turbinato, prope basin zona calycari e sepalis coriaceis acutis ad 7 mm. longis nexis cincto; vitta interzonalis suberecta 6–10 mm. longa; zona superiore circulari integra; operculo convexo 15–25 mm. longo, obtuse umbonato, intus septo persistente signato; pericarpio fusco granuloso-rugoso obsolete biloculari; seminibus plerumque 3 angulatis, apice truncatis, maturitate 15–18 mm. longis (Pl. 21, f. 2).

Type, *Krukoff 1531*, collected Dec. 5, 1931, on “terra firma” near Angustura, near the source of the Jatuarana River, Machado River region, State of Matto Grosso. Another collection from the same locality is *Krukoff 1550*. *Krukoff 1382*, collected near Tabajara in the same region, also represents the species. The two latter specimens bear the mature fruit above described. The flowers are noted as white, the local name as “Matá-matá.” Possibly this is the same species described by Miers as *Jugastrum subcinctum*, of which only the fruit is known. However, in the present species (although at anthesis numerous ovules are observed) apparently only 3 or 4 seeds mature, while the seeds of *Jugastrum subcinctum* are said to be many. The pyxidium here described is very similar to that described and figured by Miers. The truncate-based pyxidia and the nearly basal calycalis zones of *E. truncata* and *Jugastrum subcinctum* distinguish them from other species of the section.

Couratari macrosperma A. C. Smith, sp. nov. Arbor excelsa glabra ad 35 m. alta, trunco 1–1.5 m. diametro; ramis ramulisque teretibus striatis cinereis vel juventute fuscis; foliis prope apices ramulorum brevium alternatis, petiolis crassis nigrescentibus rugosis profunde canaliculatis 7–9 mm. longis, laminis coriaceis oblongis vel obovato-oblongis, 11–20 cm. longis, 5–9 cm. latis, basi acutis, apice rotundatis et breviter acuminatis vel cuspidatis, margine leviter crenatis, inter costam et margines sulculis 2–4 angustis curvis longitudinalibus signatis, pinnatinerviis, costa prominentissima, nervis lateralibus primariis 17–22 in quoque latere rectis patulis prope margines anastomosantibus; inflorescentiis desideratis; pyxidio cylindrico-conico, 15–23 cm. longo, zona calycari 7.5–10.5 cm. diametro 6-gona leviter elevata interrupta, vitta interzonalis suberecta 1–2 cm. longa, operculo laevi 7–9 cm. diametro centro leviter depresso, columella crassa subtriquetra; seminibus compressis oblongo-lanceolatis, circiter 13 cm. longis et 2.5 cm. latis, scuto embryonifero centrali circiter 6 cm. longo et 1.2 cm. lato, ala membranacea cincto (Pl. 22, f. 1, 2).

Type, *Krukoff 1513*, collected Dec. 3, 1931, on “terra firma” near Tabajara, upper Machado River region, State of Matto Grosso. The collector

notes that the plant is locally known as "Tauary." It is a species related to *C. glabra* Camb., of southern Brazil, from which it differs by its larger leaves and larger pyxidium, by its smooth rather than sulcate operculum, and by its seeds, which are three times as long and differently shaped. It may also be related to *C. Tauari* Berg, of which neither fruit nor flowers are known, but which is said to have long-acuminate leaves with fewer nerves than the present species.

Couratari Krukovii A. C. Smith, sp. nov. *C. macrospermae* affinis, habitu et foliis simillimis, sed pyxidio et seminibus differt; pyxidio conico-ellipsoideo, 11–14 cm. longo, ad medium 5.5–7 cm. diametro, zona calycari 4–5.5 cm. diametro 6-gona continua, sepalis coriaceis saepe persistentibus, vitta interzonalis convexa angustissima 3–5 mm. longa, operculo 3–3.5 cm. diametro centro depresso, columella crassa triquetra 8–10 cm. longa; seminibus compressis obovato-oblongis, 8–9 cm. longis, 2.5–3 cm. latis, scuto embryonifero centrali 4.5–5 cm. longo et 1.2–1.5 cm. lato, ala membranacea cincto (Pl. 22, f. 3, 4).

Type, *Krukoff 1653*, collected Dec. 22, 1931, on "terra firma" near the source of the Jatuarana River, Machado River region, State of Matto Grosso. The local name is noted as "Tavary," which is probably interchangeable with "Tauary." In foliage there is practically no difference between this species and the preceding, except that the leaves of *C. macrosperma* average slightly larger. The two species seem very distinct from others of the genus by the conspicuously longitudinally furrowed leaves, and also the fruits are not to be confused with any already described. The two species differ from one another markedly in fruit characters: *C. macrosperma* has a very large pyxidium broadest near the mouth, a calycalis zone of which the sepals are nearly suppressed and distinct from one another, a broad suberect interzonal band, and oblong-lanceolate seeds five times as long as broad; *C. Krukovii* has a smaller pyxidium contracted at the mouth, a calycalis zone of which the sepals are comparatively large and interconnected, a narrow flat interzonal band, and obovate-oblong seeds three times as long as broad. The pyxidium of *C. glabra* is the same shape as that of *C. macrosperma*; the seeds of *C. glabra* resemble those of *C. Krukovii*.

CARINIANA MICRANTHA Ducke. Matto Grosso: near Tabajara, upper Machado River region, *Krukoff 1439*. The local name "Tauary" is noted by the collector, whose specimens are from a tree 35 meters tall and 1.5 meters in diameter near the base. The wood is noted as very hard, it having taken two men one day to fell the tree.

CARINIANA KUHLMANNII Ducke. Matto Grosso: near Tabajara, upper

Machado River region, *Krukoff* 1375. A second collection, not far from the type locality. The name "Tauary" is also applied to this tree, according to Mr. Krukoff.

MELASTOMATACEAE

Loreya strigosa Gleason, sp. nov. Arbor 12 m. alta; rami floriferi cinerei glabri, superiores foliosi dense villosi, pilis curvatis brunneis basi incrassatis 3 mm. longis; folia ternata in quoque verticillo satis inaequalia, petiolo villosa 5–8 mm. longo, membranacea oblongo-lanceolata abrupte acuta vel subacuminata, infra medium longe cuneata irregulariter denticulata vel subintegra et quasi ciliata, nervis marginalibus tenuibus praetermissis 3-pli-nervia, supra parce scabro-hirsuta et ad costam strigosa, subtus hirsutula, venis supra planis et obscuris, subtus prominentibus, secundariis sub angulo 70° orientibus, tertiariis atris reticulatis; fasciculae ternatae ad axillas foliorum delapsorum, quaque sub-10-flora; pedicelli 3–7 mm. longi dense strigosi; hypanthium campanulatum, 4.8 mm. longum dense strigosum, pilis subulatis incurvis circiter 1 mm. longis; calycis tubus erectus 2.2 mm. longus sicut hypanthium strigosus; sepala semicircularia e sinibus angustis acutis 1.8 mm. longa, extra breviter strigosa vel ad marginem subglabra, intus sericea; petala 5 ovato-oblonga 10–11 mm. longa 4 mm. lata obtusa, extra ad basin sericea ceterum strigosa; stamina 10 isomorpha; filamenta crassa complanata glabra 7 mm. longa ad apicem sensim dilatata; antherae oblongae 6.5 mm. longae obtusae 4-loculares poris 2 minutis terminalibus dehiscentes, connectivo simplici; ovarium toto inferum 5-loculare, ovulis numerosis, summo concavum; stylus glaber sulcatus 7 mm. longus, stigmatе ovoideo.

Type, *Krukoff* 1593, collected Dec. 21, 1931, in a very old clearing near the source of the Jatuarana River, State of Matto Grosso. The vernacular name is "Jambo."

The genera *Bellucia* and *Loreya* are weakly separated. According to Cogniaux the former bears axillary flowers and the stamens are 2-pored, while the latter bears flowers on the old wood and the stamens are 1-pored. There is also a distinct difference in the general aspect of the plant, depending primarily on pubescence, leaf-shape, and character of the hypanthium. In bud the petals of *Loreya* are imbricated in such a way that they appear acute and at once suggest the related genus *Henriettella*. The anthers are distinctly 1-pored in *Loreya mespiloides*, the second species to be described, and possibly in other species as well. In *Loreya ovata* they are distinctly 2-pored; so are they in certain Peruvian and Bolivian specimens of recent collection which have been tentatively referred to *Loreya Spruceana*, and they are apparently 2-pored in Spruce's type of the latter as well.

Within the genus, *L. strigosa* is obviously related to *L. Spruceana*, but differs from it in its hirsute stems, its narrower hirsute ternate leaves, its

strongly strigose hypanthium, its longer sepals, and its narrower strigose petals. The size of the leaves varies from 36–61 cm. long by 8–18 cm. wide; the lateral nerves arise 4–12 cm. from the base of the petiole.

Loreya quadrifolia Gleason, sp. nov. Arbor 8 m. alta; rami foliiferi dense villosi, pilis brunneis 3–5 mm. longis patentibus vel sursum curvatis; rami defoliati glabrati; petioli sicut rami villosi, 3–5 mm. longi; laminae tenues, oblongo-oblanceolatae, 15–22 cm. longae, 5–8 cm. latae, subiter acuminatae, margine paullum undulatae, a medio ad basin angustam sensim cuneatae, utrinque pilosae, pilis subrigidis circiter 2 mm. longis, infra ad costam densius pilosae pilis longioribus, 3-plici-nerviae, nervis lateralibus 3–5 cm. supra basin orientibus, venis omnibus supra obscuris, subtus paullum elevatis, secundariis sub angulo circiter 60° adscendentibus, inter se 6–8 mm. dissitis; flores 5-meri subsessiles ad nodos defoliatos dense fasciculati; hypanthium late campanulatum, 5 mm. longum, densissime hirsutum, pilis 2–4 mm. longis, patentibus vel subrecurvatis, e basibus contiguus papillosis; calycis tubus 2.8 mm. longus, suberectus; sepala late triangulari-semicircularia, 2.2 mm. longa, 5 mm. lata; calyx extra ubique hirsutus hypanthio similis, intus densissime sericeus; petala ad anthesin patentia, triangulari-lanceolata, 11–12 mm. longa, 4–4.5 mm. lata, acuta, ad basin tenuia glabra, superne incrassata extra ad medium dense strigosa marginibus glabra inflexa; stamina isomorpha; filamenta 6.7 mm. longa, apicem versus incrassata; antherae crassae oblongae 4-loculares, poris 2 minutis dehiscentibus, connectivo elevato nec appendiculato nec producto; ovarium inferum parvum 5-loculari, ovulis numerosis; stylus 19 mm. longus, superne sensim dilatatus, stigmate ovoideo 2 mm. longo.

Type, *Krukoff 1510*, collected Dec. 3, 1931, on “terra firma” near Tabajara, upper Machado River region, State of Matto Grosso. *L. quadrifolia* is undoubtedly closely related to *L. strigosa*, described above, differing from it in its leaves in whorls of four, its longer, stiffer, and more spreading pubescence, its hirsute hypanthium and calyx, and its much longer style.

MYRSINACEAE

Weigeltia glomerulata A. C. Smith, sp. nov. Arbor 10 m. alta, trunco 7–8 cm. diametro; ramulis teretibus, cortice cinereo striato juventute densissime fusco-pulverulento mox glabrescente; petiolis plerumque glabris striatis leviter canaliculatis distaliter anguste alatis 15–30 mm. longis; laminis papyraceis viridibus glabris densissime minute pellucido-punctatis, ovatis vel elliptico-ovatis, 15–25 cm. longis, 6–12 cm. latis, basi attenuatis, apice subacutis vel obtusis, margine integris et cartilagineis, costa supra impressa subtus prominente, nervis lateralibus primariis 8–11 in quoque latere arcuato-adscendentibus supra planis subtus prominentibus, venulis copiose reticulatis; inflorescentiis axillaribus vel e ramulis infra folia breviter stipitatis, subspicatis vel anguste paniculatis, 2–9 cm. longis, ramulis minute ferrugineo-pulverulentis;

bracteis deciduis lanceolatis 2 mm. longis extra pulverulentis; floribus subglabris 4-meris sessilibus in glomerulis aggregatis; sepalis membranaceis plerumque epunctatis ovatis rotundatis circiter 1 mm. longis et latis; petalis velut sepalis sed leviter majoribus, basi connatis; staminibus quam petalis brevioribus, filamentis ad 0.3 mm. longis, antheris subglobosis circiter 0.5 mm. diametro, apice rotundatis, basi cordatis, per rimas longas dehiscentibus; ovario minuto conico glabro, stylo brevi; fructu nigrescente globoso ad 4 mm. diametro, stylo persistente coronato.

Type, *Krukoff 1144*, collected Sept. 16, 1931, in high forest drained by the Cupary River, on the plateau between the Xingu and Tapajos Rivers, State of Pará. It is a species of the Section *Euweigeltia* Mez, in which it is related to *W. Schomburgkiana* Mez. The longer petioles, broader leaves, and narrower inflorescences distinguish *W. glomerulata* from the Guiana species. The flowers of the new species (on our specimen not fully mature) are unusually minute; the filaments are shorter than the anthers, while *W. Schomburgkiana* has them 2–4 times as long.

Weigeltia multiflora A. C. Smith, sp. nov. Frutex dioicus gracilis erectus 0.5 m. altus, cortice fusco; foliis comatis, petiolis crassis ad 1 cm. longis fusco-puberulis, laminis chartaceis olivaceis obovatis, 45–65 cm. longis, 10–16 cm. latis, basi longe attenuatis, apice acutis et mucronatis, margine integris saepe undulatis, utrinque (praecipue subtus) lineolatim striatis et parce ferrugineo-pulverulentis, supra saepe glabris, costa utrinque prominente supra canaliculata, nervis lateralibus primariis 15–18 in quoque latere arcuato-adscendentibus utrinque elevatis, venulis copiosissime reticulatis utrinque leviter elevatis, ramulis ultimis liberis; inflorescentiis ♂ axillaribus paniculatis stipitatis multifloris, ad 25 cm. longis et 8 cm. latis, ferrugineo-pulverulentis, ramulis bracteis papyraceis puberulis oblongis acutis 6–10 mm. longis subtentis; floribus 3-meris basi decidue bracteolatis; pedicellis velut ramulis pulverulentis, 2.5–4 mm. longis; sepalis vix ultra $\frac{1}{3}$ connatis anguste imbricatis ovatis rotundatis, 1–1.2 mm. longis et latis, punctis magnis nigrescentibus pictis, margine membranaceis et arcte fimbriatis; petalis velut sepalis pictis oblongis, 4.5–5 mm. longis, 2–2.5 mm. latis, apice obtusis, margine glabris, maturitate recurvatis; staminibus quam petalis brevioribus prope basin insertis, filamentis carnosius 2 mm. longis apice gracilibus, antheris subglobosis 0.6–0.8 mm. diametro, dorso glandulosis, apice rotundatis, basi cordatis, per rimas dehiscentibus; ovarii rudimento minuto globoso ferrugineo-pulverulento; floribus ♀ ignotis.

Type, *Krukoff 1388*, collected Nov. 23, 1931, on “terra firma” near Tabajara, upper Machado River region, State of Matto Grosso. Another collection from the same region is *Krukoff 1377*. It is a species of the Section *Triadophora* Mez, based on the Colombian *W. Schlimii* (Hook. f.)

Mez. In common these plants have 3-merous flowers and extraordinarily robust leaves and inflorescences, together with noticeable subepidermal sclerenchyma fibers. Their relationship with other species of *Weigeltia* does not seem very close. Compared with *W. Schlimii*, *W. multiflora* has a simpler habit, the leaves entire rather than toothed, and the inflorescence simply rather than twice pinnate. In flower structure there is little difference, although the new species has narrower petals and strictly glabrous anthers.

SAPOTACEAE

Lucuma inflexa A. C. Smith, sp. nov. Arbor mediocris; ramulis teretibus fuscis vel cinereis, juventute ferrugineo-sericeis mox glabrescentibus; petiolis mox glabris rugosis canaliculatis, 7–12 mm. longis, basi nigrescentibus et incrassatis; laminis chartaceis glabris oblongis, 8–12 cm. longis, 3–5 cm. latis, basi cuneatis, apice acuminatis (apice ipso obtuso), margine integris, nervis lateralibus primariis 7–9 in quoque latere arcuato-adscententibus, cum costa supra subplanis subtus elevatis, venulis reticulatis subtus prominulis; inflorescentiis in nodis fasciculatis 2–5-floris; pedicellis gracilibus 25–40 mm. longis, superne incrassatis, densissime ferrugineo-sericeis; calyce velut pedicellis extra sericeo, intus minutissime pulverulento, sepalis 5 late imbricatis inaequalibus, exterioribus carnosis deltoideo-ovatis, circiter 4 mm. longis et 5 mm. latis, interioribus submembranaceis oblongis, circiter 3 mm. latis; corolla campanulata tenuiter carnosae extra sericeae intus glabra 5–6 mm. longa, lobis 5 tubum subaequantibus ovatis, 3–3.5 mm. latis, apice rotundatis; staminodiis late ovatis inflexis, 1.5 mm. longis et latis, apice obtusis; staminibus (saepe anantheris) basi loborum insertis, filamentis carnosis minutis (0.5 mm. longis), antheris valde inflexis ovoideis, 2 mm. longis, 1 mm. latis, 4-alatis, apice apiculatis, per rimas extrorsas dehiscentibus; ovario dense sericeo depresso-globoso plus minusve 6-lobato, loculis 3, ovulo 1 in quoque loculo; stylo tereti ovarium aequante, apice minute 3-lobato.

Type, *Krukoff 1505*, collected Dec. 3, 1931, on "terra firma" near Tabajara, upper Machado River region, State of Matto Grosso. The plant is locally known as "Cramary;" the inner bark is said to yield a white latex. It is a species of the Section *Rivicoa* A. DC., related to *L. retusa* Spruce and *L. obscura* Huber. With the latter it has in common a 3-celled ovary. *L. inflexa*, however, has the leaves somewhat smaller and the pedicels longer than *L. obscura*. The staminodes of the present species are obtuse and the anthers practically sessile, in which points it also differs from *L. obscura*. Flowers in which the anthers are completely lacking are very common, many of the closed buds which were dissected showing this feature. The specific name refers to the strongly inflexed anthers.

Lucuma platyphylla A. C. Smith, sp. nov. Arbor 20 m. alta, trunco 25–30 cm. diametro; ramulis subteretibus crassis densissime ferrugineo-velutino-

tomentosis demum glabrescentibus; petiolis tomentosis crassis leviter canaliculatis, 15–40 mm. longis; laminis chartaceis bullatis obovato-oblongis, 18–30 cm. longis, 8–12 cm. latis, basi acutis, apice caudato-acuminatis vel cuspidatis, margine integris et leviter revolutis, supra praeter costam glabris, subtus pilis ferrugineis erectis stipitatis 2–4-ramosis 0.5 mm. longis pubescentibus, costa supra subplana subtus prominentissima, nervis lateralibus 13–16 in quoque latere patulis, prope margines anastomosantibus, supra impressis subtus prominentibus, venulis copiosissime reticulatis supra prominulis subtus elevatis; floribus 3–8 in fasciculis ad nodos infra folia; pedicellis gracilibus 12–16 mm. longis, densissime ferrugineo-tomentosis; sepalis 5 uniseriatis basi connatis deltoideo-ovatis, circiter 3 mm. longis et latis, apice acutis, extra velut pedicellis tomentosis, intus minute flavescenti-sericeis; corolla submembranacea flavida glabra circiter 6 mm. longa, lobis 5 tubum aequantibus ovatis rotundatis 2.5–3 mm. latis, margine saepe sinuatis; staminodiis carnosis ovatis, circiter 2.5 mm. longis et 1.5 mm. latis, apice acuminatis; filamentis fertilibus carnosis 1–1.5 mm. longis, antheris inflexis ovoideis, 2 mm. longis, 1.2 mm. latis, basi cordatis, apice obtusis; ovario depresso-globoso circiter 2 mm. diametro, dense tomentoso (pilis ad 0.7 mm. longis), valde 5-costato, loculo unico non centrali, ovulo unico; stylo quam ovario brevior, minute lobato.

Type, *Krukoff 1316*, collected Nov. 12, 1931, on "terra firma" near Tabajara, upper Machado River region, State of Matto Grosso. The plant is locally known as "Abiurana;" the inner bark yields a white latex. It is a species related to *L. ramiflora* (Mart.) A. DC., which it resembles in habit, pubescence, and inflorescence. However, *L. platyphylla* has the leaves much larger, the flowers 5- rather than 4-merous, and the ovary 1- rather than 2-celled. The numerous ovaries I have dissected show only one locule containing one ovule; the single locule is not central, and the distinctly 5-costate ovary indicates that the other 4-locules are abortive.

Lucuma anibaefolia A. C. Smith, sp. nov. Arbor glabra 10 m. alta, trunco 15 cm. diametro; ramulis teretibus striatis, juventute stramineis; petiolis saepe violaceis canaliculatis, 6–12 mm. longis; laminis olivaceis chartaceis oblongis, 10–17 cm. longis, 2.5–5 cm. latis, basi subattenuatis, apice obtuse acuminatis, margine integris saepe sinuatis, costa utrinque prominente, nervis lateralibus primariis 12–14 in quoque latere arcuato-adscendentibus supra subplanis subtus elevatis, venulis copiosissime reticulatis utrinque prominulis; inflorescentiis 5–10-floris, floribus fasciculatis, pedicellatis (pedicellis gracilibus 3–5 mm. longis, flavescenti-puberulis), basi bracteatis, bracteis deltoideis acutis ad 1 mm. longis; calyce extra puberulo intus glabro, sepalis 6 imbricatis subaequalibus ovatis obtusis, 1–1.5 mm. longis et latis, margine membranaceis et fimbriatis; corolla submembranacea glabra breviter campanulata 2 mm. longa, lobis 6 tubum subaequantibus ovatis obtusis 1 mm. latis, margine fimbriatis; staminodiis ovatis inflexis, circiter 0.6 mm. longis, apice acutis;

staminibus prope basin tubi adnatis, filamentis 0.3 mm. longis, antheris ovoideis, circiter 0.5 mm. longis, parcissime puberulis, per rimas laterales dehiscentibus; ovario depresso-globoso, sub anthesi 1 mm. diametro, minutissime sericeo, loculo unico, ovulo unico; stylo carnoso, circiter 0.7 mm. longo, apice truncato.

Type, *Krukoff 1447*, collected Nov. 25, 1931, on varzea land along river, near Tabajara, upper Machado River region, State of Matto Grosso. A local name is "Abiuhy." It is a species probably best placed in the Section *Eremoluma* (Baill.) Engl., because of its 1-celled 1-ovuled ovary, although 6-merous flowers have not previously been noted in the section. It is related to *L. rostrata* Huber, but has proportionately narrower leaves, a more compact inflorescence, and much smaller flowers than that species.

EBENACEAE

Diospyros Melinoni (Hiern) A. C. Smith, comb. nov. *Maba Melinoni* Hiern, Trans. Cambr. Phil. Soc. 12: 143. 1873.

Examination of an isotype of this species in the herbarium of the New York Botanical Garden indicates that the ovary is habitually 8-celled and the styles 4. It belongs, therefore, in the genus *Diospyros*, Section *Rospidios* Hiern. Its nearest relative is apparently *D. glomerata* Spruce. In leaf texture and flower structure the two species are very similar, but *D. Melinoni* has leaves only half as large, the flowers less densely aggregated, and the floral pubescence sparser. *D. glomerata* has the corolla densely sericeous rather than essentially glabrous.

The species has been collected by Krukoff (no. 1188) in high forest drained by a tributary of the Cupary River, on the plateau between the Xingu and Tapajos Rivers, State of Pará. As this specimen bears ♂ flowers, the following description may be appended to the original:

♂ inflorescence axillary, short, 2-6-flowered, the peduncles up to 3 mm. long; flowers subsessile, subtended by sericeous oblong bracts about 2 mm. long; calyx flavo-sericeous on both sides, about 5 mm. long including lobes, the lobes 5 or 6, deltoid, acute, 2.5-3 mm. long, about 1.5 mm. broad; corolla white, rotate, 5- or 6-lobed nearly to the base, the lobes thin-carnose, obovate, 5-6 mm. long, 3-4 mm. broad, rounded at apex and frequently recurved, sericeous towards the base without, glabrous within; stamens 45-55, lightly coherent at base, the filaments 0.5-0.8 mm. long, setose with hairs about 1 mm. long, the anthers oblong-linear, acute, curved, about 2 mm. long, setose at apices and on connectives; ovary apparently completely lacking.

Diospyros Krukovii A. C. Smith, sp. nov. Frutex 3-4 m. altus; ramulis teretibus cinereo-pulverulentis demum glabrescentibus, internodiis 2.5-4.5

cm. longis; petiolis canaliculatis 7–12 mm. longis, velut ramulis decidue pulverulentis; laminis chartaceis siccitate fuscis oblongis, 15–25 cm. longis, 5.5–8 cm. latis, basi rotundatis et abrupte cuneatis, apice longe acuminatis (apice ipso obtuso), margine integris et leviter recurvatis, utrinque glabris (vel subtus juventute parce flavescenti-strigosis), nervis lateralibus 8–10 in quoque latere arcuato-adscententibus, cum costa supra elevatis subtus prominentibus, venulis copiose reticulatis utrinque leviter elevatis; floribus ut videtur semper hermaphroditis axillaribus solitariis subsessilibus, basi bracteatis, bracteis 3–5 ovatis, 5–6 mm. longis, 4 mm. latis, extra strigosis intus glabris; calyce ubique dense flavescenti-sericeo, fere ad basin 5-lobato, lobis deltoideo-ovatis acutis, 6–7 mm. longis, 3–4 mm. latis; corolla subrotata alba tenuiter carnosam mox decidua profunde 5-lobata, lobis prope bases imbricatis ovato-oblongis subacutis, 8–10 mm. longis, 4–5 mm. latis, extra lineis latis pilorum pallidorum vestitis, intus glabris; staminibus uniseriatis circiter 16 distinctis, ad basin corollae adfixis; filamentis stramineis glabris carnosius circiter 1 mm. longis; antheris oblongo-linearibus acutis 5 mm. longis, connectivis pilos pallidos setosos ad 1.5 mm. longos gerentibus; ovario globoso densissime strigoso (pilis 2 mm. longis); stylis 3 basi connatis, 3.5 mm. longis, divaricatis, stigmatibus in lobis 3 planis irregularibus breviter fimbriatis divisis; loculis 6, ovulo 1 in quoque loculo; fructibus globosis, maturitate 2.5–3.5 cm. diametro, persistenter strigosis, pericarpio coriaceo, seminibus maturitate 2 vel 3 ovalibus circiter 15 mm. longis et 8 mm. latis.

Type, *Krukoff 1564*, collected Dec. 7, 1931, on “terra firma” near Angustura, near the source of the Jatuarana River, Machado River region, State of Matto Grosso. According to Hiern’s monograph, *D. Krukovii* would fall into the genus *Maba*, Section *Tricanthera*, by virtue of its 5-merous flowers and 6-celled ovary. In this section, it resembles *M. sericea* (A. DC.) Hiern in its solitary hermaphrodite flowers. Two recent students¹ have considered *M. sericea* best placed in *Diospyros*, where it constitutes a rather anomalous species in the Section *Rospidios* Hiern. This treatment is here followed.

From the species of this alliance, *D. sericea* A. DC., *D. pseudoxylopia* Mildbr., and *D. dichroa* Sandwith, the new species is readily distinguished by having its leaves fully twice as large and essentially glabrous beneath, as well as by floristic details. *D. Krukovii* apparently always has the flowers perfect, whereas the above mentioned species are said to be dioecious or polygamo-dioecious. The fact that the subequal stamens are attached to the corolla in a single row is also a point upon which *D. Krukovii* agrees with neither *Maba* nor *Diospyros*, as they are commonly understood.

¹ Mildbr., Notizbl. 10: 195. 1927; Sandwith, Kew Bull. 1931: 483. 1931.

APOCYNACEAE

Prestonia Lindleyana Woodson, nom. nov. *Haemadictyon calycinum* Lindl.; Miers, Apoc. So. Am. 259. 1878; not *Prestonia calycina* Muell. Arg. (1860).

Matto Grosso: Near Tabajara, upper Machado River region, *Krukoff* 1427.

Prestonia trifida (Poeppig) Woodson, comb. nov. *Haemadictyon trifidum* Poeppig; P. & E. Nov. Gen. & Sp. 3: 67. *pl.* 275. 1845.

Matto Grosso: Near source of the Jatuarana River, Machado River region, *Krukoff* 1545.

Odontadenia Hoffmannseggiana (Steud.) Woodson, comb. nov. *Echites grandiflora* G. F. W. Mey. Fl. Esseq. 131. 1818; not Roxb., Roth, Stadelm., or Hoffmsg. *Echites macrantha* R. & S. Syst. 4: 795. 1819; not Spreng. *Echites Hoffmannseggiana* Steud. Nom. ed. 2. 1: 539. 1840. *Odontadenia speciosa* Benth.; Hook. Journ. Bot. 3: 242. 1841.

Matto Grosso: Near Tabajara, upper Machado River region, *Krukoff* 1457, 1471.

VERBENACEAE

Aegiphila villosissima Moldenke, sp. nov. Frutex scandens; caulibus et ramis crassis medullosis obtuse tetragonis densissime longeque villosis, pilis fuscis vel ferrugineis patentibus vel reflexis 4–8 mm. longis; ramulis gracilioribus; internodiis valde elongatis 9–18 cm. longis; foliis oppositis; petiolis crassis 5–10 mm. longis dense longeque villosis; laminis laete viridibus membranaceis ovatis vel ovato-ellipticis 11.5–25 cm. longis, 4.5–12 cm. latis, ad apicem abrupte breviterque acuminatis, margine integris et longe ciliatis (pilis subsetosis) saepe subrevolutis, ad basin insigniter rotundatis, utrinque dense villosis, pilis fuscis subsetosis circa 3 mm. longis et plerumque usque ad 1 mm. dissitis; costa supra plusminus impressa, subtus perprominente, utrinque dense villosa praecipue subtus; venis secundariis gracilibus 10–12 in quoque latero arcuato-adscendentibus insigniter 5–17 mm. a margine anastomosantibus dense villosis; inflorescentiis axillaribus terminalibusque paniculatis; panicula terminali bracteata circa 10 cm. longa et 5.5 mc. lata 5-cymifera, ubique dense longeque villosa; paniculis axillaribus longe pedunculatis paniculae terminali consimilibus vel parvioribus et subcymosis; cymis conspicue bracteolatis; pedunculis crassiusculis 2.5–6 cm. longis, ubique sicut ramulis dense longeque villosis; bracteis paucis lanceolatis circa 1 cm. longis et 4 mm. latis, ad apicem et basin attenuatis, utrinque densissime longeque villosis; bracteolis linearibus elongatis usque ad 17 mm. longis dense villosis; calyce levi herbaceo circa 1.5 mm. longo et 3.3 mm. lato patentissimo e basi campanulato, extra dense longeque villosa, intus glabro, margine 4-lobato, lobis brevi-

bus obtusis; corolla infundibulariformi, tubo (immaturo?) anguste cylindrico circa 1.5 mm. longo glabro, lobis 4 oblongo-lingulatis 3.8–4 mm. longis circa 2.5 mm. latis obtusis glabris; staminibus 4 ad oram tubi corollae insertis; filamentis (immaturis?) filiformibus circa 0.7 mm. longis, inferne pilosis; antheris oblongis circa 1.3 mm. longis et 0.7 mm. latis; stylo capillari circa 2.6 mm. longo glabro; ramulis stigmatis bifidi circa 2 mm. longis valde patentibus; ovario depresso-oblongo circa 1 mm. longo et 1.3 mm. lato, ad apicem umbilicato et 4-sulcato, 4-loculare.

Type, *Krukoff 1400*, collected Nov. 23, 1931, on "terra firma" near Tabajara, upper Machado River region, State of Matto Grosso. The species is most closely related to the Peruvian *A. cordata* Poepp. The latter, however, differs in its much smaller and distinctly subsessile leaves whose blades are conspicuously cordate or subcordate at the base and in its short-pedunculate or subsessile cymes and lack of axillary panicles. Its flowers, also, are much larger than in our species, but in ours the flowers are not yet quite open, so that their dimensions may be unreliable.

SOLANACEAE

Solanum quaesitum Morton, sp. nov. Subg. *Leptostemonum*, Sect. *Oliganthes*; frutex erectus ca. 4 m. altus; rami superiores robusti, ca. 6 mm. diametro, leviter sulcati, pilis stellatis subferrugineis longe stipitatis crebris obtecti, aculeis recurvatis ca. 5 mm. longis, ca. 3 mm. basi latis, apice acutis, parce pubescentibus armati; folia superiora solitaria; petioli pro magnitudine laminae sat longi, ca. 32 mm. longi, dense pubescentes, pilis stellatis longe stipitatis vestiti, aculeati, aculeis rectis usque 1 cm. longis basi perspicue pubescentibus; laminae ovatae, usque ad 23 cm. longae et 17 cm. latae, vix vel evidenter 5 lobatae, basi inaequaliter rotundatae, in petiolum haud decurrentes, apice acutiusculae, membranaceae, utrinque (in statu sicco) olivaceae, supra pilis stellatis pauciradiatis longe stipitatis (cum pilis minoribus simplicibus apice glanduliferis intermixtis) crebre vestitae, venis lateralibus primariis ca. 5, supra paullum impressis, subtus prominentibus; inflorescentiae extra-axillares, a foliis remotae, ca. 8-florae; pedunculus communis ca. 5 cm. longus; pedicelli ca. 15 mm. longi, densissime pubescentes, pilis longissime stipitatis; calyx 5-partitus, lobis reflexis, lanceolatis, ca. 17 mm. longis, coriaceis, margine membranaceis erosis, intus glabris, extus in tota superficie densissime pubescentibus, pilis stellatis, pauciradiatis, longissime stipitatis, stipitibus robustis usque 5 mm. longis, lutescentibus; corolla violacea (sec. Krukoff), rotata, magna, explanata ca. 5 cm. lata, plicata, 5-lobata, lobis lanceolatis acutis, extus dense tomentosis (pilis stellatis vix stipitatis), intus in vena media parce pubescentibus, fere usque ad apices membranarum interpetalariis glabris conjunctis; filamenta ca. 2 mm. longa, glabra; antherae lineari-lanceolatae, ca. 13 mm. longae, 1.5 mm. latae, poris apicalibus minutis; ovarium subglobosum, glabrum; stylus rectus, stamina fere aequans, glaber; pedicelli fruc-

tiferi ca. 3 mm. diametro; calyx fructiferus auctus, ca. 2.5 cm. latus, valde et irregulariter incrassatus, setis sparsis persistentibus; bacca globosa, ca. 4 cm. diametro, glabrata; semina obovoidea vel suborbicularia, ca. 3 mm. diametro, testa favosa.

Type, *Krukoff 1637*, collected Dec. 20, 1931, in a new clearing near the source of the Jatuarana River, Machado River region, State of Matto Grosso. Closely allied to *Solanum setosicalyx* Rusby, which differs in the indument of the upper leaf surface being scabrous and composed of numerous stout simple hairs, rather than stellate-tomentose and glandular as in the present species. Rusby in his description of *S. setosicalyx* does not indicate the relationship of the species even as to the section. Examination of a specimen of the type collection¹ in the U. S. National Herbarium shows, however, that it belongs to the section *Oliganthes*, and is near or probably synonymous with the earlier *Solanum Vanheurckii* Muell. Arg.,² known to me from the original description only.

Solanum placitum Morton, sp. nov. Subg. *Pachystemonum*, Sect. *Anthoresis*; frutex erectus, ca. 6 m. altus; rami juniores angulati, scabriusculi, pilis minutis ochraceis stellatis sessilibus vel breviter stipitatis pleniradiatis sat densis praediti; folia solitaria; folia minora axillaria ("auriculae") desunt; petioli foliorum inferiorum usque 3 cm. longi, superiorum subnulli, pubescentia eae ramulorum simili; laminae obovatae, magnae, maximae saltem 34 cm. longae et 16.5 cm. latae, integrae, apice breviter et acute acuminatae, basi longe cuneatae et in petiolum decurrentes, membranaceae, utrinque (in statu sicco) olivaceae, concolores, supra juventute parce strigosae, pilis pro parte maxima simplicibus subulatis basi inflatis apice acicularibus usque 0.25 mm. longis, ca. 0.5 mm. distantibus, pro parte minima (praecipue in venis mediis et lateralibus) stellatis minutis sessilibus pauciradiatis, demum glabratae, tunc pilis 1–3 mm. distantibus, subtus persistente stellato-puberulentae, pilis minutis, sessilibus pauciradiatis, 0.25–0.5 mm. distantibus, venis lateralibus primariis ca. 7, subtus elevatis; inflorescentiae terminales pauciflorae; pedunculus ca. 6 cm. longus, apice furcatus, sicut ramuli pubescens; pedicelli ca. 5 mm. longi, dense stellato-tomentosi, apice non incrassati; calyx subturbيناتus, 5-dentatus, ca. 4 mm. longus, 7 mm. latus, extus densissime stellato-tomentosus, pilis minutis sessilibus vel brevissime stipitatis, intus glaber (pilis paucis apicem versus exceptis), venulosus, dentibus deltoideis aequalibus ca. 2 mm. longis, ca. 2 mm. basi latis, apice acutis; corolla alba (sec. Krukoff), rotata, explanata, ca. 17 mm. lata, 5-fida, lobis ovalibus ca. 6 mm. longis apice acutis, extus in tota superficie dense stellato-tomentosis, intus glabris, tubo brevi, ca. 2 mm. longo, glabro; filamenta ca. 2 mm. longa, glabra, basi in

¹ Huachi, head of Beni River, Bolivia, *H. H. Rusby* (Mulford Amazon Expedition) 451.

² Van Heurck, Obs. Bot. 85. 1870.

tubum saltem 0.5 mm. altum connata; antherae late ellipticae, ca. 3 mm. longae, 2 mm. latae, poris magnis introrsis; ovarium globosum, dense stellato-hirsutum; stylus curvatus, ca. 7 mm. longus, 0.6 mm. crassus, pilis paucis stellatis instructus; fructus deest.

Type, *Krukoff 1583*, collected Dec. 20, 1931, in a very old clearing near the source of the Jatuarana River, Machado River region, State of Matto Grosso. The present plant does not appear to be closely related to any of the previously described species of the section *Anthoresis*. It belongs to the general group of species related to *S. verbascifolium* L. The character of the pubescence of the upper surface of the leaves, however, is characteristic, as are also the monadelphous stamens and the shape of the leaves.

RUBIACEAE

Coussarea machadoana Standl., sp. nov. Arbor 14-metralis, trunco 30 cm. diam., praeter inflorescentiam omnino glabra, ramulis crassiusculis rectis subteretibus, internodiis elongatis; stipulae 4–5 mm. longae in vaginam brevem incrassatam persistentem connatae, lobis brevissimis apiculatis; folia maxima breviter petiolata coriacea in sicco flavescentia, petiolo crasso 1–1.6 cm. longo; lamina anguste elliptico-oblonga c. 28 cm. longa et 9 cm. lata apice obtusa at 1 cm. longe caudato-cuspidata, acumine obtuso, basi acuta, costa supra elevata, nervis prominentibus, subtus paullo pallidior, costa valde elevata, nervis lateralibus utroque latere c. 14 prominentibus angulo fere recto divergentibus marginem attingentibus leviter arcuatis, venulis vix prominulis reticulatis, margine plus minusve revoluta; inflorescentia terminalis cymoso-paniculata sessilis basi trichotoma dense multiflora 9 cm. longa 14 cm. lata, ramis rectis crassiusculis minutissime pruinoso-puberulis, floribus aggregatis cymulosis vel interdum subumbellatis crasse 1–2 mm. longe pedicellatis, bracteis obsoletis; hypanthium globoso-obovoideum 1–1.5 mm. longum pruinoso-puberulum, calyce truncato 1 mm. alto 2 mm. lato; corolla alba extus glabra in alabastro apice acuta, tubo crassiusculo 8–9 mm. longo apicem versus angustato, lobis 4 lineari-lanceolatis 5–6 mm. longis apicem angustum versus sensim attenuatis intus minute puberulis patentibus; antherae inclusae; stylus gracilis rectus glaber 2.5–3 mm. longus, ramis c. 1 mm. longis.

Type, *Krukoff 1361*, collected Nov. 15, 1931, on "terra firma" near Tabajara, upper Machado River region, State of Matto Grosso. The species is a well-marked one because of its remarkably large leaves, much greater in dimensions than in most members of the genus.

Elaeagia brasiliensis Standl., sp. nov. Arbor, ramulis teretibus brunneo-ochraceis crassis, novellis dense puberulis; stipulae ovato-triungulares 6–8 mm. longae persistentes puberulae cuspidato-acuminatae; folia mediocria

coriacea breviter petiolata, petiolo crasso 6–12 mm. longo pilosulo vel glabrato; lamina elliptica vel late elliptica vel rotundato-obovata 8–12 cm. longa 4–9.5 cm. lata obtusa vel apice saepe rotundata basi acuta vel late cuneato-obtusa, supra glabra lucida, subtus fere concolor ad nervos sparse pilosula vel fere omnino glabra in axillis parce barbata, costa elevata, nervis lateralibus utroque latere c. 5 elevatis angulo acuto adscendentibus valde obliquis fere rectis, venulis prominulis arcte reticulatis; inflorescentia terminalis cymoso-paniculata sessilis et e basi trichotoma vel interdum 8 cm. longe pedunculata, dense multiflora, 5–12 cm. longa et aequilata vel latior, ramis brunnescentibus rigidis adscendentibus vel subpatentibus dense minute puberulis, floribus aggregatis sessilibus vel breviter crasse pedicellatis, bracteis deciduis; capsula 4 mm. longa et aequilata obovoideo-globosa dense minute puberula septicidalis, valvis apice saepe breviter bifidis; semina pauca minuta anguste alata, alis laciniatis.

Type, *Krukoff 1018*, collected Sept. 6, 1931, in high forest on “terra firma” at Fordlandia, Tapajos River region, State of Pará. Because of the absence of flowers, there is some uncertainty regarding the generic position of this tree, but the fruit characters and those of the foliage agree better with *Elaeagia* than with any other group. No species of that genus have been reported heretofore from Brazil, although they are to be expected there.

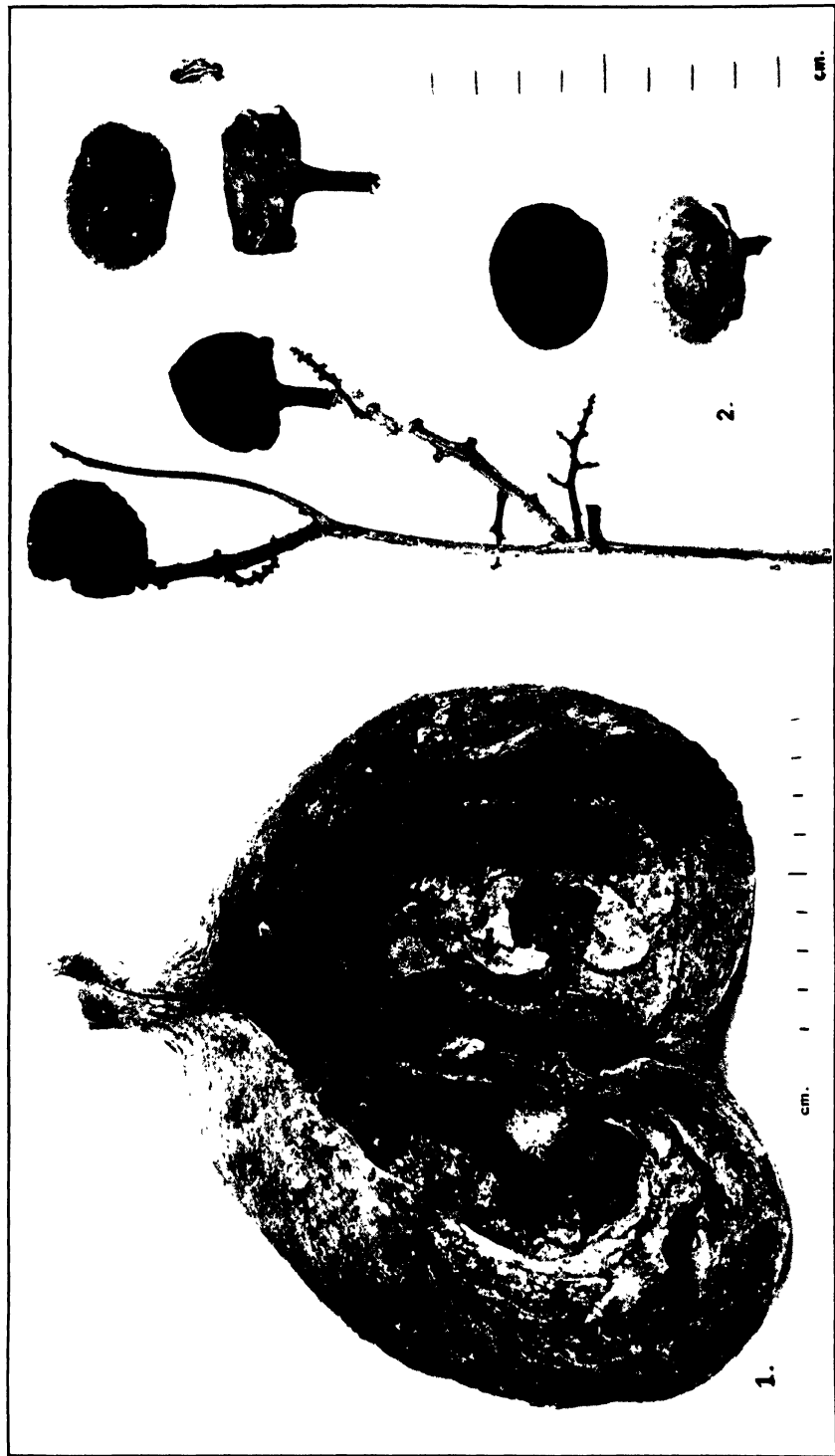
Explanation of plates 21, 22

Plate 21

1. Fruit of *Sterculia megalocarpa*.
2. Old inflorescence and fruits of *Eschweilera truncata*.

Plate 22

1. Seed of *Couratari macrosperma*.
2. Pyxidium of *Couratari macrosperma*.
3. Pyxidium of *Couratari Krukovii*.
4. Seed of *Couratari Krukovii*.



GLEASON AND SMITH STERCULIA ESCHWEILERA



GLEASON AND SMITH COURATARI

Pollen-tube behavior in *Hemerocallis* with special reference to incompatibilities

A. B. STOUT AND CLYDE CHANDLER

(WITH PLATE 23 AND SEVEN TEXT FIGURES)

In the various daylilies (*Hemerocallis*) seed-production to self-pollination ranges from complete failure due to incompatibility in fertilization to a high degree of self-fertility with many individuals and clons that are only feebly self-compatible and for which seed-production to self- or close-pollination is always low. Quite the same grades of seed-production are also seen in cross-fertilizations. The daylilies are perennials, spreading by crown-branching or by rhizomes to give well-established plants or groups of plants and hence numerous flowers are easily obtained for any plant or for plants of the same clon. The pistils of the flowers are, for certain types, as much as 10.5 cm. in length and fertilizations that are compatible are usually completed in 24 hours or less.

Thus the daylilies afford excellent material for determining pollen-tube growth (1) in various grades of self- and cross-incompatibility, (2) after premature and delayed pollinations and (3) after inter-specific cross-pollinations, and the degree of fruit and seed production following each kind of pollination is readily determined in controls. A very brief mention of the pollen-tube behavior in *Hemerocallis* has been made (Stout, 1931a). The present paper will present the data in detail with graphs for various curves of growth.

MATERIALS AND METHODS

In obtaining material for study, as a rule as many as 50 flowers of a single clon that had opened under glassine bags were pollinated at one time, usually at or near 9:00 A.M. It is at this time that the anthers of most flowers of the diurnal daylilies are fully dehiscing and the pistils are receptive to compatible fertilizations. At intervals thereafter, at least three flowers were removed and their pistils preserved for study. For premature pollination, delayed pollination and pollination of the flowers of night-blooming sorts, applications of pollen were made at other hours.

In the study of the pollen tubes in the pistils the paraffin method was utilized, but mostly a method of direct dissection and staining was employed as already described in considerable detail (Chandler, 1931; Stout, 1931b). The pistils are preserved in a solution of 100 c.c. of 70% alcohol and 6 to 8 c.c. of commercial formalin (37%). In staining, the pistils are dissected and a few drops of aceto-carmin (saturated solution in 45% acetic acid) are made to flow the entire distance of the style. After a few

seconds a drop of magenta (1% aqueous solution) or a drop of aceto-carmin to which has been added a trace of ferric acetate is placed on the style. The excess stain is removed with absolute alcohol. Glycerine and a cover glass complete a preparation which may be kept for study for a period of several months.

With the use of a microscope the extent of the growth of the pollen tubes in the various pistils is determined and tabulated. If tubes extend into the lower part of the style the ovary is also sectioned and stained. By this method it is rather easy to determine the position of the ends of the pollen tubes, their distribution in the pistil, and their appearance. The pistils of the various kinds of daylilies differ somewhat in length. For example, the styles of the *H. Thunbergii* range from 7 to 8 cm. in length, and those of the *H. fulva* clon Europa range from 9.2 to 9.6 cm. in length. In plotting the extent of pollen-tube growth in these plants the style of a pistil is divided into ten equal units and thus the data for numerous pistils differing somewhat in length may be presented in the same type of graph.

STRUCTURE OF PISTILS AND COURSE OF POLLEN TUBES

The long slender styles of the pistils of daylilies taper toward the stigma which is slightly expanded into three somewhat definite lobes with the surface covered with elongated papillae (plate 23, figs. 2, 3). Within the style a canal (the "Leitkanal" of Behrens, 1875) extends continuously from the stigmatic surface to the ovary chambers (plate 23, fig. 8). The center of the face of the stigma is somewhat funnel-shaped and the opening into the canal is narrow and almost closed by the interlocking of papillae. A short distance below the stigma the canal increases in diameter and occupies about one-third the diameter of the style (plate 23, figs. 4, 5). For a considerable distance the canal is somewhat three-lobed in the outline of a cross section and there are three narrow strips of irregular cells extending vertically along the wall in the relative position of the placentae, but between these the canal is lined with a layer of somewhat enlarged cells which, however, present a smooth surface. There is no specialized conducting tissue at any point through which pollen tubes travel endotropically. The continuous canal which extends through the style and into the ovary chambers allows any secretions that may be formed to mingle somewhat freely, and it is possible that secretions from the ovary may travel upward to some distance on the wall of the canal.

The stigmatic surface of the pistil of *Hemerocallis* is covered with long slender papillae. In the bud shortly before the flower opens these papillae are erect and turgid. Microscopic examination shows that a

spirally creased layer of cutin covers a thick layer of mucilage which surrounds the cytoplasm of each papillate cell. When the flowers open the papillae spread apart somewhat, especially at their tips. (plate 23, fig. 2). Some of the tips of the papillae become enlarged, the folds become irregular in size bulging in places, and a few small droplets can be seen along the creases of the folds. Soon a thin film of secretion covers the exterior of the papillae thus spreading over the exposed surface. This condition prevails for the time during which pollen is first shed and pollination is accomplished. But soon the papillae near the center of the stigma collapse and the mucilage appears to be liberated near the base of the end cells of the papillae. Toward the end of the day a few papillae around the outer edge of the stigma may still be turgid but the papillae over most of the stigma are collapsed and considerable secretion is released.

Pollen tubes pass over and between the papillae of the stigmatic surface and enter the stylar canal and then travel on into the ovary without being compelled to penetrate through tissues. The ends of the pollen tubes frequently linger in the vicinity of the ovary and in some cases there is later a resumption of growth in this region. Such responses suggest a very direct action of chemotactic substances originating from the ovary or its ovules. In only a few cases here reported was there any swelling of the ends of some of the tubes followed by bursting.

In daylilies large numbers of pollen tubes are usually not present within the styles even when there is a high degree of self-fruitfulness as this is judged by the production of large capsules well filled with seeds. There appears to be a fundamental condition which restricts the number of tubes which enter the stylar canal.

The graphs which follow show the extent to which at least several tubes and usually a number of tubes penetrated at the various time-intervals. In most cases the data for the curves of growth are remarkably consistent.

DATA ON GROWTH OF POLLEN TUBES

Pollen-tube growth in Hemerocallis fulva clon Europa. The fulvous day-lily, *H. fulva* clon Europa, is completely self-incompatible (Stout, 1921; 1926). This clon is a triploid with much mixiploidy fluctuating about a chromosome number of 33, (3×11), (Stout, 1932). There is much abortion of pollen but some pollen is viable and functional in fertilizations and for this there is complete self-incompatibility in that capsules do not even start to develop to self-pollination. This clon is strictly diurnal in habit of blooming and all "normal" pollinations were made at or near the hour of 9:00 A.M.

Several thousand self-pollinations and intra-clonal-pollinations have been made for various plants of this clon obtained from many localities in Europe and America. In every case there was *no enlargement* of the ovaries and the flowers promptly abscised. When inter-specific cross-pollinations are made, using pollen of *H. Thunbergii* or *H. citrina*, the ovaries begin to enlarge and they usually remain attached to the pedicel for at least 10 days, toward the end of which many of the capsules quickly wither and soon fall. Only a very few of such capsules remain to maturity and give viable seeds. Of a total of about 10,000 such cross-pollinations

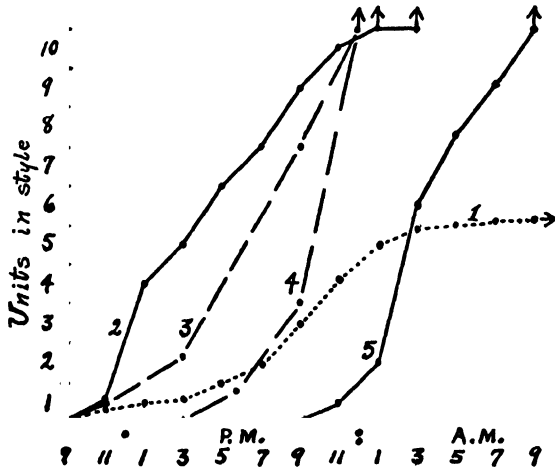


Fig. 1. Curves for pollen-tube growth for the Europa daylily: (1) selfed, normal pollination; (2) $\times H. Thunbergii$, normal pollination; (5) $\times H. Thunbergii$, delayed pollination; (3) $\times H. aurantiaca$, normal pollination; (4) $\times H. aurantiaca$, somewhat delayed.

made to date only 31 capsules have matured and the largest number of seeds having embryos that were obtained in any capsule has been five (Stout, 1926, fig. 4). In this case the failure to yield capsules and seeds more abundantly to inter-specific cross-pollinations is obviously due to the very marked abortion of macrospores and not merely to a lack of affinity in the relations of fertilization or to the failure of pollen tubes to reach the ovary. The low production of seeds after various cross-pollinations is not due fundamentally to selective fertilization, but to macrospore abortion which follows the abnormalities in sporogenesis. There are hence in this clon two types of sterility, one involving abortion of spores and one involving self-incompatibility in the reactions of pollen tubes of microspores that do not abort.

As shown in figure 1, in the Europa daylily the pollen tubes from self-pollinations penetrate only to about half the length of the styles. From the 6th to the 16th hour a slow rate of growth is rather uniform but almost no advance is made thereafter. Pollen tubes are however not abundant at the lowest point of penetration, and the majority of the tubes remain in the region of the stigma. The ends of the tubes are as a rule only slightly swollen and enlarged.

When the pollen of *H. Thunbergii* is used in cross-pollination on the Europa daylily there is a rapid advance of tubes during the 3rd and the 4th hours, then there is a rather steady rate of growth with, however, a slower rate during the two hours before the ovary is entered. Sixteen hours after pollination pollen tubes are found within the cavity of the ovary in ample time for abundant fertilization. Capsules begin to develop to nearly every flower thus pollinated, but seeds rarely mature after such pollinations evidently because of the abortion of macrospores.

When pollen of *H. Thunbergii* was used in delayed pollination, made 12 hours after the usual time of pollination (i.e. at 9:00 P.M. instead of 9:00 A.M.) the pollen tubes grew somewhat more slowly during the first four hours and then continued at a more rapid pace and were within the ovary at the end of 12 hours. But even in this case the most rapid rate of advance was between the 2nd and the 6th units of measurement of the styles and not in the basal half.

The advance of pollen tubes in styles of the Europa daylily after normal pollination and after a delayed pollination of six hours with pollen of *H. aurantiaca* is also shown in text figure 1. There was a rather uniform acceleration in the growth of the more advanced tubes until they were found within the ovary 15 hours after pollination. At this time, however, the majority of the tubes were in the uppermost quarter of the style, others were scattered at different levels below and only a few entered the ovary. This condition also prevailed three hours later. In delayed pollinations of flowers in the same set of flowers made at 3:00 P.M. or six hours later than the normal pollinations the rate of growth was greater, the acceleration was more pronounced, and the more advanced tubes were in the ovary after 9 hours of growth and at the same hour of the day when pollen tubes of normal pollination reached the ovary. No seed has been obtained from any of these cross-pollinations.

In premature pollination with pollen of *H. aurantiaca* made at 9:00 P.M. on the evening before a set of flowers opened and 12 hours before normal pollination, the pollen remained on the stigma but failed to germinate and penetrate into the pistil until almost the hour for normal pollination. Collections of pistils thus prematurely pollinated were not made after 26

hours, but at that hour of the day the pollen tubes were somewhat more advanced than for normal pollination. This result is not represented in figure 1.

Studies were also made of pollen-tube behavior when pistils of the Europa daylily were decapitated at various levels and pollen applied to the exposed end of the part left with the ovary. When only the stigmas were removed for self-pollination there was some germination of pollen and penetration of the pollen tubes but none grew better or extended further than when the stigmas were not removed. When the upper four-fifths of the style was removed and self-pollen applied to the cut surface a

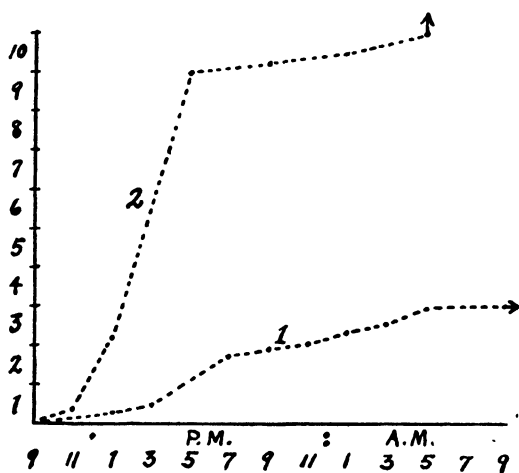


Fig. 2. Curves for pollen-tube growth: (1) of *H. fulva* clon *Maculata*, selfed, which is completely self-incompatible, and (2) for a wild plant of *H. fulva* selfed, which is somewhat self-compatible.

few pollen tubes grew through the lower part of the style and extended into the ovary but none were found entering a micropyle. Pollen of *Hemerocallis Thunbergii* was also applied to pistils cut to one-fifth their length, but in no case did pistils thus treated give mature capsules with seeds.

Pollen-tube growth in the H. fulva clon Maculata. This garden clon has been in cultivation since 1897 and it originated either from a seed or from a living plant sent from Shen-si, China to Florence, Italy. This clon is triploid with $3n = 33$ chromosomes, but it is quite distinct from the older Europa daylily, in having larger flowers and slightly different coloration (for colored plate and history, see Stout, 1929). There is much abortion of pollen and there is complete self-incompatibility, for the pollen tubes which do develop penetrate only a short distance down the stylar canal

(fig. 2). In certain cross-pollinations with other types of fulvous daylilies and especially with all triploids thus far tested the clon *Maculata* is completely seedless. In cross-pollination with plants of *H. citrina* as many as fifteen seeds have been obtained in a capsule.

Pollen-tube behavior in a wild plant of H. fulva. A wild plant, *H. fulva*, obtained directly from the interior of China has been rather highly self-compatible in that numerous capsules with from 1 to 15 seeds each are obtained to selfing. The study of a set of pistils indicates that the pollen tubes from selfing (fig. 2) advance rapidly and at a very uniform rate from 2 to 8 hours when they are almost at the opening of the ovary. Then they

TABLE 1

*Results of successive self-pollinations of one large plant of Hemerocallis Thunbergii**

DATES OF POLLINATION	JUNE		JULY															TOTALS
	28	30	1	3	5	7	8	10	11	12	13	14	15	17	18			
No. flowers	4	14	11	15	6	14	7	16	19	7	5	11	10	6	8	153		
No. complete failures	4	11	5	6	6	10	5	12	13	4	2	4	5	3	4	94		
No. rudimentary capsules		2	2	2		1	1	1	1	1	1	2	2	2	1	19		
No. mature capsules		1	4	7		3	1	3	5	2	2	5	3	1	3	40		
No. seeds per capsule		3	1-3	1-4		1-4	3	1-4	1-2	1-3	1	1-2	1-4	1	1-2	80		

* This plant of *H. Thunbergii* bloomed from June 28 until July 18. A total of 150 flowers were self-pollinated, 91 ovaries soon fell, 19 remained to form dry empty capsules, and 40 gave a total of 80 seeds, the number ranging from 1 to 4 per capsule. This is typical of results thus far obtained with all daylilies that are feebly self-compatible.

linger in this position for about 12 hours before they enter the ovary. This is a striking case of a delay of pollen-tube growth at the opening into the ovary followed by the advance of some tubes into the ovary and some fertilization.

Pollen-tube growth in Hemerocallis Thunbergii. The clon of *H. Thunbergii* studied is one that has been in general garden culture since 1890 (Stout, 1929, for colored plate and description). It is diploid ($2n = 22$), the pollen is highly potent, and capsules and seeds are readily produced to certain crosses. After self-pollinations the rule is that the perianths are shed leaving the ovaries which soon begin to enlarge. Many of these ovaries absciss from 7 to 26 days after pollination; others remain attached though they shrivel to small dried structures (Stout, 1921, fig. 8), and about one-third of all flowers pollinated will yield capsules which mature and contain from 1 to 5 seeds each with occasionally as many as eight seeds. Such capsules require from 40 to 55 days to mature. There is no cyclic mid-period or end-period self-compatibility, for the production of these capsules is

distributed throughout the entire period of flowering as is shown in the data in table 1. The maximum number of seed is always very low, quite as is characteristic of many cases of partial compatibility.

After normal self-pollination in the clon of *H. Thunbergii* studied, the rate of pollen-tube growth is very rapid during the 5th, 6th, 7th, and 8th hours at the close of which the ends of tubes are within 1 cm. of the ovary. But they linger in this region for about 8 hours and are first found within the ovary at the end of 18 hours after pollination. There is only slight swelling of the ends of the pollen tubes and there is evidently no

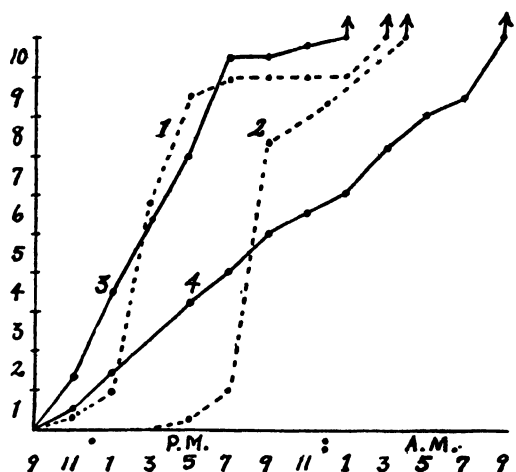


Fig. 3. Curves for pollen-tube growth for *H. Thunbergii*: (1) selfed, normal; (2) selfed, delayed; (3) \times *H. aurantiaca*, normal; (4) \times *Europa* daylily, normal.

bursting. Here an inhibition in the advance of the tubes takes place near the entrance to the ovary. But tubes finally enter the ovary and at least some fertilizations may result to give the few seeds obtained.

Pollen-tube behavior was studied after delayed self-pollinations made six hours later than normal. For these, the pollen tubes grew slowly during the first four hours, then there was a rapid growth for two hours during which nearly seven-tenths of the style was traversed, and then the growth was decidedly retarded during the 7 to 9 hour period. No collections were made between the 9th hour and the 13th hour at the end of which many tubes were within the ovary. After delayed self-pollination the tubes reach the ovary more quickly than after normal self-pollination due to more rapid growth during the 4–6 hour interval and to less retardation in the region of the ovary.

After inter-specific-pollination with pollen of *H. aurantiaca* the rate

of pollen-tube growth is rapid during the first ten hours at the close of which the ends of the tubes are less than 0.5 cm. from the upper end of the ovary. But the ends of the tubes remain in this position and do not enter the ovary until some six hours later. This cross readily yields capsules and viable seeds. In certain crosses on this clon of *H. Thunbergii* nearly every flower that is pollinated yields capsules filled with seeds, the number of which has been as high as twenty-three, a result which demonstrates that the ovules are highly able to function when there is the proper fertilization.

When the pistils of this plant are pollinated with pollen of the *H. fulva*

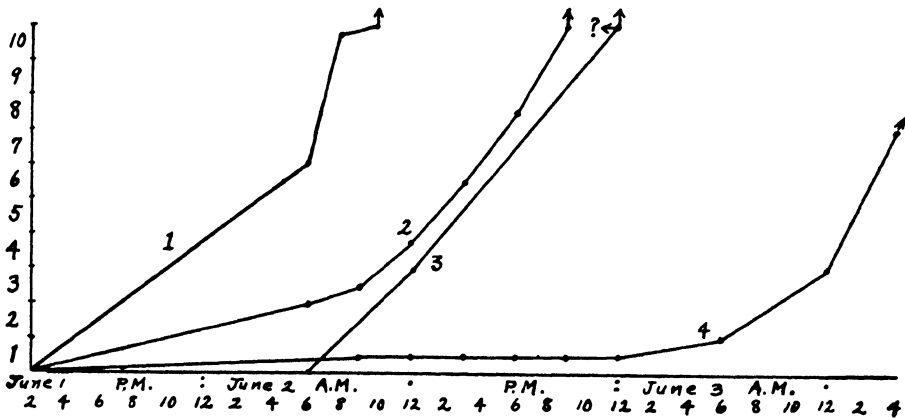


Fig. 4. Curves of pollen-tube growth for *H. flava*: (1) delayed pollination on flowers fully open on June 1; (2) premature pollination of set to fully open on June 2; (3) normal pollination of set fully open on June 2; (4) very premature pollination of set to open on June 3rd.

clon Europa the pollen tubes grow steadily but at a much slower rate for a period of 22 hours when there is an acceleration which brings them into the ovary at the end of 24 hours. But fertilization does not readily occur or at least few capsules with viable seeds mature. Of 1895 flowers of this cross only 8 capsules matured and the number of seeds per capsule ranged from 1 to 5, but thus far no seedlings have been reared from such seed.

Pollen-tube behavior in Hemerocallis flava. The clon of *H. flava* which was studied (Stout, 1929) is highly self-fruitful for it produces fine large capsules well filled with viable seeds to almost every flower that is self-pollinated. It is obviously a different clon from that of the *H. flava* studied by Focke (1893) which was reported to be self-fruitless, and also from that studied by Jost (1907) which was feebly self-fruitful. The description of Jost for the self-sterility of the plant he called *H. flava* applies almost

exactly to the results seen in *Hemerocallis Thunbergii*. Some of the seedlings of the clon here studied appear to be self-incompatible, and so there may be many incompatibilities within this species and in the genetical nature of the clon here studied. The particular clon studied is, however, highly self-fruitful as far as the production of seeds to selfing is concerned. Plants of this clon of *H. flava* bloom early in spring. During warm weather the sets of flowers open in the late afternoon and continue in excellent condition throughout the following day. With cooler weather the sets may not start anthesis until in the early forenoon. A single set may remain open and fairly fresh for a period of 50 hours.

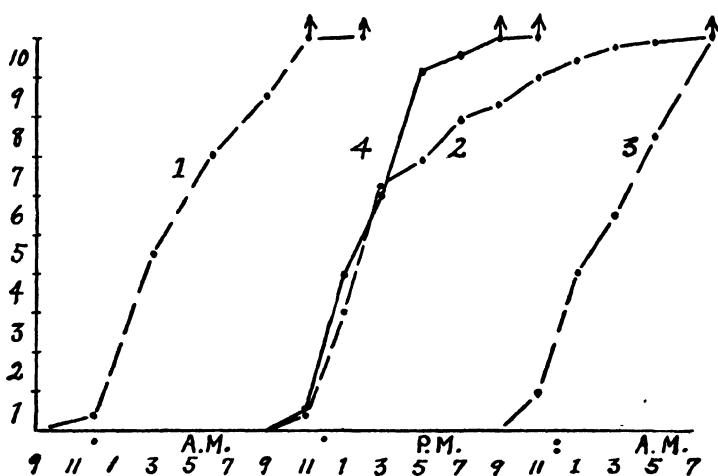


Fig. 5. Curves of pollen-tube growth for an F_1 hybrid (Ser. 6 #1) of *H. flava* \times *H. fulva* clon Europa: (1) selfed, premature; (2) selfed, normal; (3) selfed, delayed; (4) \times a sister hybrid, normal.

In this clon the data from two collections of pistils after a self-pollination at 6:00 A.M. of flowers open for that day indicate that pollen tubes are within the ovary at least at the end of 18 hours. Special studies were made for premature self-pollinations and these showed that while some grains promptly germinate the tubes grow slowly until about the time of the early forenoon when normal pollinations occur. This was very marked in the case of a premature pollination on June 1st of flowers that were open on the day of June 3rd.

*Pollen-tube behavior in the two F_1 hybrids of *H. flava* \times *H. fulva* clon Europa.* Pollen-tube behavior was determined for two of the F_1 seedlings (Ser. 6 #1 and Ser. 64 #2) obtained by crossing *H. flava* as a seed parent with the Europa daylily. These seedlings are therefore hybrids between

two distinct species and of the individual plants used as parents one is self-fruitful and the other is self-incompatible.

The hybrid, Ser. 6 #1, is very feebly self-compatible; from many self-pollinations only two seeds have been obtained. As shown in text figure 5, the pollen tubes of normal self-pollinations grow rapidly from 2 to 6 hours after pollination; then their rate is retarded and they grow much more slowly and a few enter the ovary only after 22 hours. A set of flowers was also utilized in delayed self-pollination; flowers were emasculated and bagged, and the pollen from other flowers was saved from forenoon until 9:00 P.M. when the delayed pollinations were made. For these pollinations

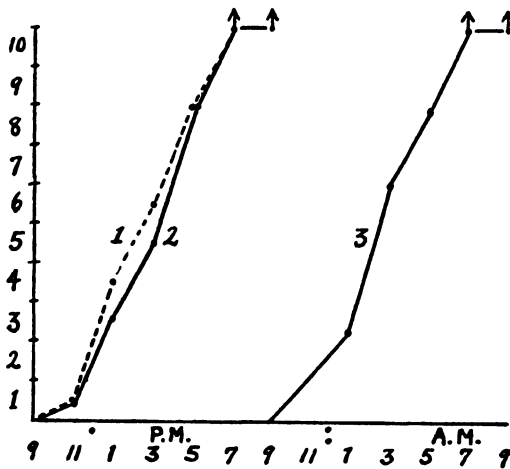


Fig. 6. Curves of pollen-tube growth for a hybrid (Ser. 64 #2) of *H. flava* \times *H. fulva* clon Europa: (1) selfed, normal; (2) $\times H. Thunbergii$, normal; (3) $\times H. Thunbergii$, delayed.

the tubes continued at a rather rapid and uniform pace and without delay entered the ovary after 10 hours of growth at the same hour (7:00 A.M.) of the day when the tubes of pollinations made ten hours earlier on the same day (at 9:00 A.M.) entered the ovary.

After premature self-pollination the pollen tubes grow at a rather rapid rate after the first two hours and enter the ovary within a period of 14 hours yet no seed was produced to the controls of such pollinations. In this plant the normal pollinations result in much delay of pollen tubes in the region near the ovary, while in premature and in delayed pollination there is no such delay.

When the plant 6 #1, which is diploid, is pollinated with pollen of its triploid pollen parent, Europa, the pollen tubes penetrate only about one-

tenth of the length of the style and hence no fertilizations result. This is a very complete cross-incompatibility with the pollen-tube growth completely inhibited in the apical portion of the style.

The hybrid 64 #2 rarely sets a seed to self-pollination, yet the pollen tubes grow rapidly and steadily beginning with the 3rd hour and at the end of the 10th hour are within the ovary (text figure 6). Here is a most striking case of reaction of self-incompatibility within the ovary. When crossed in normal pollination with *H. Thunbergii* the tubes grow almost as in the selfing and enter the ovary after the same interval of time, but in

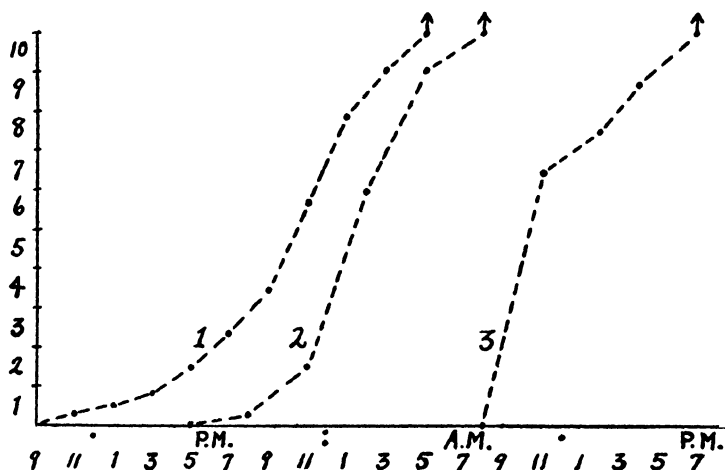


Fig. 7. Curves of pollen-tube growth for the night-blooming *H. citrina*: (1) selfed, premature; (2) selfed, normal; (3) selfed, delayed.

this case there is the development of capsules with numerous viable seeds. The curve for pollen-tube growth after delayed cross-pollination with *H. Thunbergii* is almost identical with that for normal pollination.

Judged by seed production to controlled self-pollination the two sister plants, 6 #1 and 64 #2, are equally self-incompatible but the pollen-tube behavior for normal pollinations is very different; for 6 #1 there is inhibition of growth in the region immediately above the ovary; for 64 #2 there is no delay in the advance of tubes and the incompatible reactions occur within the ovary. But in premature and in delayed self-pollination of 6 #1 the behavior is quite the same as that of 64 #2 for normal pollination.

Pollen-tube behavior in Hemerocallis citrina. Several different clons have been received under the name *Hemerocallis citrina* but the one studied was obtained from Willy Müller in Naples from the garden (Hortus Nucerenensis) from which this species was first distributed to the trade, and this

clon is said by Mr. Müller to be a division of the stock first described as *H. citrina* (for history, description and colored plate see Stout, 1930). This clon is decidedly nocturnal in flowering habit; the flowers open in the evening and shed pollen during the night, but usually there is abundant pollen present in anthers the next morning. If the day is warm and sunny the perianths wilt early in the forenoon but if the weather is cool and cloudy the flowers continue more or less open and fresh until at least mid-day. For this clon normal pollinations are considered to be those made in the evening on freshly opened flowers.

The clon of this species which the authors studied is self-incompatible to the extent that very few seeds have thus far been obtained to numerous self-pollinations. Premature, normal and delayed self-pollinations were made on a single set of flowers and pollen-tube growth for each was determined.

The "normal" pollinations were made at 5:00 P.M. when pollen was shedding in freshly opened flowers. After the first three hours pollen-tube growth was fairly rapid with the maximum rate in the middle part of the style, and tubes were in the ovary at the end of 15 hours. For premature pollinations, pollen of the previous set of flowers was saved in vials and applied at 9:00 A.M. to the stigmas of flowers still in bud. For these the pollen-tube growth was somewhat slower especially in the apical portion of the pistil and the tubes entered the ovary only three hours earlier in the day than they did after normal pollination. After delayed pollination made at 8:00 A.M. the following forenoon (a delay of 15 hours) the rate of growth of tubes was very rapid for the first three hours during which three-fifths of the style was traversed. Then the rate became much slower and the tubes were in the ovary at the end of 12 hours.

It is to be noted that certain inter-species cross-pollinations on this clon of the *H. citrina* yield seeds whether pollinations are made in the evening or in the following forenoon, but that self-pollinations rarely yield seed although the tubes to normal self-pollination reach the ovary at 8:00 A.M. This result seems to indicate that the self-incompatibility in this case involves reactions within the ovary.

SPECIAL TESTS OF POLLEN-TUBE GROWTH IN CULTURES

The viable pollen grains of daylilies readily germinate on media of 5, 10, or 15 grams cane sugar, 1 gram agar agar, and 100 cc. water at room temperature. Somewhat extended studies were made of the rate and the extent of growth on media for pollen collected at different ages of the flower and at different temperatures for reactions to secretions of the pistil.

The growth of pollen tubes on artificial media and under various constant temperatures was studied for pollen of *H. citrina*, *H. Thunbergii* and *H. fulva longituba*. The best growth was obtained under constant temperatures ranging from 68° to 80° F., and tubes 1210 μ long were obtained. In all cases the rate of growth was most rapid during the first two hours and in most cases there was little or no increase in length after this period. It is to be noted that the maximum length of growth of pollen tubes on artificial media is in this case only about 1 mm., which in the pistils would scarcely more than carry tubes to the opening of the stylar canal.

Special tests for evidence bearing on chemotactic reactions were made. Pistils were placed on agar media with the stigmatic end near the center of the culture and pollen grains were scattered evenly about the stigma. Self-pollen and cross-pollen of various combinations were tested for various daylilies. In many cases there was no noticeable influence on the direction of the growth of pollen tubes. In several cases tubes in the immediate region of the stigma grew toward the stigma but this was the case for self-incompatibility as well as for cross-fertility. Sections of the style and the ovary were used in the same way as the stigma but with no definite results. Also the fluids obtained from severed styles and ovaries were drawn into fine capillary glass tubes which were placed in the midst of cultures or with one end resting near the periphery of a culture. There was excellent germination and growth of tubes but in no case was there any recognizable effect on the growth of tubes either in the length to which tubes grew or in the direction of their growth. Droplets of the fluid obtained when styles are severed were placed on slides and pollen grains were sown directly in them but the grains burst and no germination was obtained which would seem to indicate that the stylar canal of *Hemerocallis* does not contain the same fluid that is obtained when the style is severed and which evidently comes largely from the cortex.

SUMMARY AND DISCUSSION

The main aspects of pollen-tube behavior most characteristic for the compatible fertilizations after normal pollination in *Hemerocallis* may be stated as follows:—the pollen tubes travel in an open canal throughout the entire length of the pistil; a period of about two hours after pollination is usually required before tubes are noticeably within the stylar canal; the most rapid rate of pollen-tube advance is in the upper-middle portion of the style; fertilization is completed within a period of 24 hours after normal pollination.

Obviously, characters of generic specificity are responsible for many

aspects of pollen-tube behavior and for marked differences in the behavior among different genera of flowering plants. Thus for comparison, in highly compatible cross-fertilizations between plants of *Nicotiana Forgetiana* at least five days are required (East and Park, 1918, fig. 1, p. 361) for the pollen tubes to traverse styles that are only 2.0 to 2.5 cm. in length. The relatively much more rapid advance of pollen tubes in *Hemerocallis* is correlated with the longer styles, the shorter life of pistils, and possibly also with the hollow rather than the solid style. The long life of the pistils of *Nicotiana* allows pollen tubes of self-incompatible relations to continue growing for as many as 14 days (East and Park, 1918, fig. 1), a condition not possible in *Hemerocallis*.

It is to be noted that there are numerous types of selective and discriminative relations in fertilization. Inter-specific and inter-variatal relations, the relations between various polyploids, the various interactions of intra-specific incompatibilities, and the various grades of self-incompatibility are all expressed in the reactions in the pistil. The scope for pollen-tube reactions is so limited that distinctive and specific behavior can not be expected for each of the various sorts of selective action. The reactions observed may however be considered and properly related to the particular condition known to exist from experimental data.

In the various forms of *Hemerocallis* studied three distinct types of pollen-tube behavior in self-incompatibility are to be recognized:

- (1). The reactions may be complete in the upper portion of the style. In this case the tubes travel slowly and only advance to a short distance in the stylar canal. This was seen only after the selfing of the two triploid clons *Europa* and *Maculata*. The type of reaction which is expressed in the stigmatic end of the pistil has been known in the earlier studies of Jost (1907) and of Correns (1913) and in the more recent studies, especially of *Nicotiana* by East and Park (1918). Such relations in solid pistils, it would seem, involve most completely a relation between haploid pollen tubes and diploid tissues of the style. In the triploid daylilies it may be an expression of a doubling through triploidy of certain of the hereditary factors for incompatibility.

- (2). In many cases of self-incompatibility in *Hemerocallis* the pollen tubes are at or near the open entrance to the ovary in ample time for fertilization but there is then a decided inhibition in the advance of the tubes. In such cases it appears that the tubes are reacting to secretions from the ovary. In certain cases the tubes may linger or remain almost stationary for several hours and then proceed into the ovary. Possibly this reaction indicates that special inhibiting substances are no longer being produced and that any such substance produced earlier becomes in-

active. During the time when the advance of a group of pollen tubes is checked either temporarily or permanently the shorter tubes behind them do not continue to advance.

The pollen tubes in *Hemerocallis* have been examined rather carefully for any evidence of differential growth among classes of sister pollen. The pollen tubes are more or less scattered but convincing evidence of two or more different modes or levels in their distribution has not been observed. Such reactions are assumed to occur for certain cross-pollinations between plants which carry factors for incompatibility. Thus in the simpler type of incompatibility crosses between two plants which possess one factor in common (as $S_1S_2 \times S_1S_3$) only one class of pollen (the S_3) is assumed to function (see especially Lehman, 1927). Also in the type which involves qualitative and quantitative inter-relations between incompatibility factors and factors for fertility as conceived by Kakizaki (1930) differential fertilizations in certain crosses are assumed to occur. Thus in the cross $S_1S_2T_2T_2 \times S_1S_1T_1T_2$ only the S_1T_2 pollen is supposed to function. But in neither of these types of incompatibility is selective fertilization assumed to occur in selfing. Selective fertilization in selfing is, however, well known for various plants in which certain pollen-tube factors are linked with endosperm qualities that show deficiency in ratios as seen in corn (summarized by Jones, 1928). Direct observation of bimodal distribution of pollen tubes from sister pollen has been made in the case of crosses between $2n \times 2n+1$ plants of *Datura* (Buchholz and Blakeslee, 1932) and it is considered that the same differential growth occurs in selfing $2n+1$ plants. In the types of *Hemerocallis* studied differential fertilizations in selfing are not apparent in pollen-tube behavior.

(3). There are cases of almost complete self-incompatibility in which the pollen tubes proceed directly into the ovary without delay, and yet seeds are seldom formed. In this condition it is clear that the reactions of incompatibility involve either (a) the pollen tubes and the secretions of the ovary or possibly of the ovules or of the egg apparatus, or (b) the relations of sperm and egg in the final stages of fertilization, or (c) the abortion of young embryos.

When the reactions are close to or within the ovary there is obviously greater opportunity for a direct relation between haploid pollen tubes and the haploid megagametophytes, and especially when there is a stylar canal.

Reactions of incompatibility after the pollen tubes reach the ovary or enter it are to be recognized as a well-defined type of behavior. This condition has been noted in certain other plants which exhibit self-incompatibility, namely, in certain apples (Cooper, 1929) and for certain individuals

of head cabbage (Sasaoka, 1928). In the cyclic self-incompatibility of plants of *Brassica pekinensis* (Stout, 1931b) powerful reactions may operate in the first flowers to open which produce coiling of pollen tubes on the stigma but in certain later flowers the tubes may enter the ovary and yet no seeds, or only a very few seeds, result.

In a series of studies with *Petunia*, Yasuda, (1932) concludes that the substances which inhibit pollen-tube growth in the secretions of the stigma are mainly secreted in the ovary and then they move to the upper part of the stigma.

In the various cross-fertilizations studied there were no cases of inhibition of pollen in the upper portion of the style. In the cross *H. Thunbergii* × *H. aurantiaca* (fig. 3) the pollen tubes were delayed for several hours at the entrance of the ovary quite as in the selfing. For the crosses of the Europa daylily with pollen of *H. aurantiaca* and *H. Thunbergii* the pollen tubes proceed without delay into the ovary. Thus the pollen-tube behavior in the cross-relations studied shows no noticeable inhibition in the upper portion of the style. In these inter-species fertilizations factors of specificity rather than those of incompatibility are no doubt involved.

A low yield of seed, or "feeble compatibility," to certain selfings and crossings is characteristic of incompatibilities not only in daylilies but in numerous other plants. This is evident when a particular pollination which is amply and properly made very constantly gives less seeds than are possible when the seed parent and the pollen involved are used in other relations. In the daylilies this condition involves, as a rule, reactions at or within the ovary rather than merely a slow rate of growth of pollen tubes in the style. Also seeds are not increased in number by premature pollination. The studies show rather definitely that in many such cases pollen tubes reach the ovary at the time when tubes are normally attracted to the egg apparatus and when a full complement of seeds is possible. Under such conditions the low seed number can be due either to the presence in the ovary of few tubes or to reaction of incompatibility and selective fertilization in the ovules.

The behavior of pollen tubes in *Hemerocallis* makes it clear that the reactions of incompatibility may be complete in the upper part of the style as seen in a few cases, but that it is the rule that they are expressed at the entrance to the ovary or within the ovary.

A preliminary study of pollen-tube growth in several types of *Hemerocallis* was made during 1927 by Mr. T. Susa while technical assistant at the New York Botanical Garden. It was deemed advisable to extend the

studies to include other types and relations, and to make more frequent collections of a larger number of pistils in each relation and for each pollination, and this was done for the data here reported.

NEW YORK BOTANICAL GARDEN

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Explanation of plate 23

Fig. 1. Pistils of *Hemerocallis Thunbergii* (A) and of Europa daylily (B). About natural size.

Fig. 2. Stigmatic portion of pistil showing upright papillae soon after flower opens. $\times 18$.

Fig. 3. Cross section of pistil of *H. Thunbergii*, at *a* of fig. 1. $\times 35$.

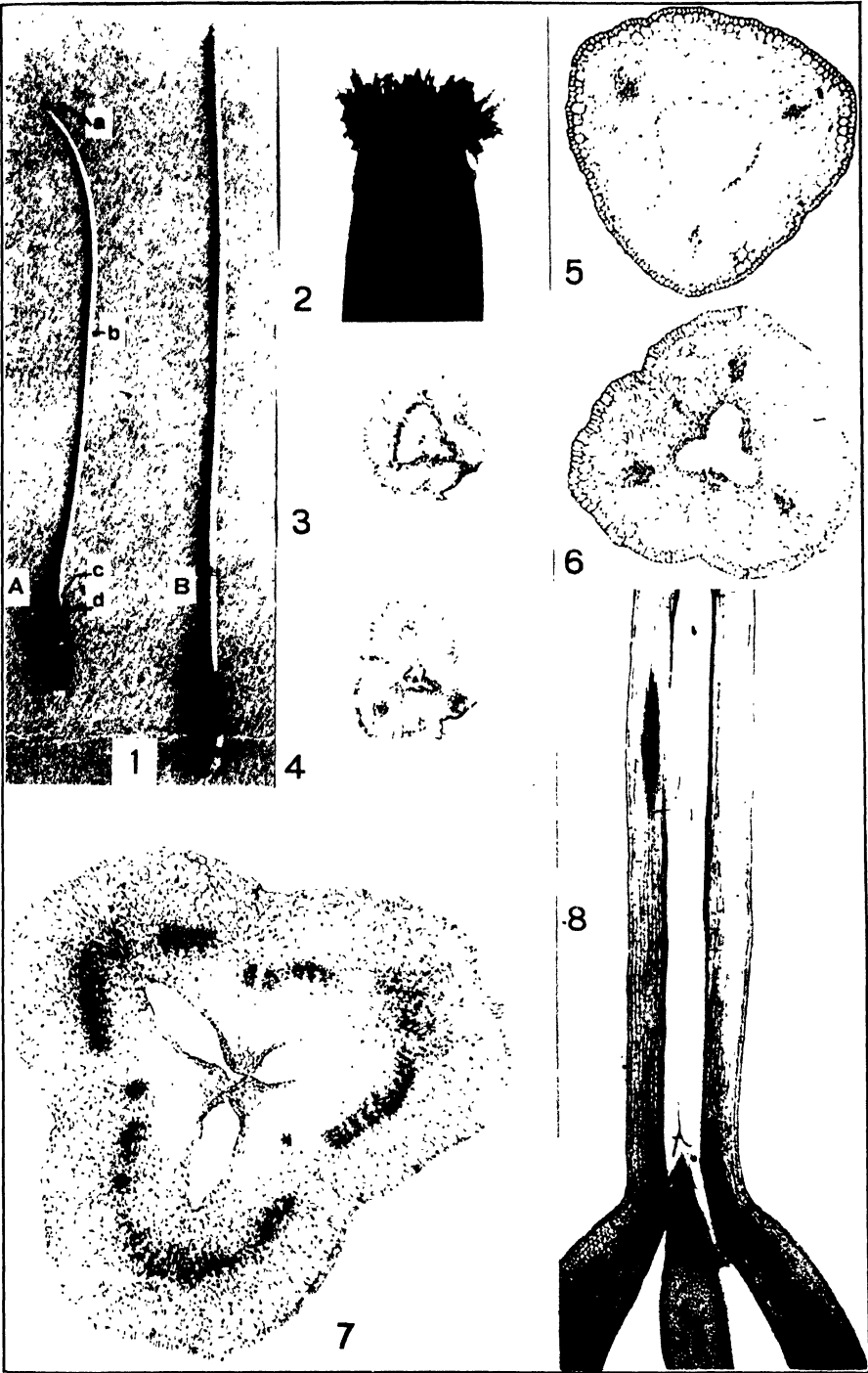
Fig. 4. Cross section of pistil just below *a* in fig. 1, at point where stylar canal is constricted. $\times 35$.

Fig. 5. Cross section of pistil at *b* of fig. 1, showing large stylar canal. $\times 35$.

Fig. 6. Cross section of pistil at *c* of fig. 1, showing entrance to the three ovary chambers. $\times 35$.

Fig. 7. Cross section of pistil at *d* of fig. 1, showing the beginning of the ovary. $\times 35$.

Fig. 8. Longitudinal section of *H. Thunbergii* pistil showing pollen tubes in the style 24 hours after self-pollination. $\times 21$.



Preparation of pollen for microscopic examination

R. P. WODEHOUSE

The question has often arisen regarding whether a wet or a dry medium is to be preferred for mounting pollen, and upon which may be placed the greater reliance—this because most kinds of pollen are extremely sensitive to changes in moisture owing to certain hygroscopic substances which they contain; and frequently there is much difference between their appearance when wet and when dry. Most kinds of pollen, except those with very thin, elastic or fragmentary exines, have their own peculiar ways of accommodating changes in volume with corresponding changes in form. Indeed, the mechanisms by which this is accomplished are enormously varied and sometimes elaborate and extremely complicated, and they show that volume-change-accommodation is a real and normal function of the exines of pollen grains.¹ And as we pass in review the pollen of any considerable number of different species of plants it becomes quite evident that the mechanisms for the accomplishment of volume-change accommodation have undergone evolutionary development comparable in extent to that of the adaptive mechanisms of flowers to pollination by insects. In all studies of pollen-grain morphology, therefore, mounting media which reveal such mechanisms must be chosen.

Most frequently volume changes are accommodated by three or more slit-like furrows in the exine. When there are only three furrows they are generally meridionally arranged, but when there are more, they may have other arrangements.² When such a grain is dry its furrows are generally closed and so far buckled inwards that not even their margins may be seen, but as soon as it is moistened and expanded its furrows open widely; then it is seen that each is crossed by a delicate furrow membrane which may or may not possess decorations of its own, but is usually marked at its center by a germinal aperture of varying shape, and through which a germinal papilla bulges, and occasionally each furrow is crossed by an underlying transverse furrow. Since the opening of the furrow, therefore, reveals the furrow margins, the germinal aperture and papilla, and the transverse furrow when present, a grain that is expanded is enormously more interesting and instructive than one that is dried and collapsed, and in which none of these things can be seen.

It should be stated at this juncture that this view is by no means universally accepted. All of the earlier investigators believed that pollen could be satisfactorily observed only in its "dry and natural" form, in

¹ Wodehouse, R. P. *Ann. Bot.* **42**: 896. 1928.

² Wodehouse, R. P. *Bull. Torrey Club* **57**: 21–46 1930.

ignorance of the fact that the wet and the dry forms are equally natural. The impression of the unnaturalness of the forms assumed by pollen grains when wet was corrected by von Mohl³ in 1835 and he also showed that much more could be seen in them in their moist than in their dry condition. Very recently, however, my work has been severely criticized by botanists of eminence in their own field for having been done with grains in their expanded form. Ferguson and Coolidge,⁴ in their studies upon petunia pollen, state: "In his studies of pollen grains, Wodehouse (1928) used as mounting media either an alcohol-water-glycerine combination or Brandt's glycerine jelly. . . . From the data presented in the present paper it seems clear that both dry air and balsam as mounting media give a truer picture of the size and form of pollen grains than does any aqueous medium." And again: "As a result of our observations it is believed that descriptions of pollen grains, as observed in an aqueous medium are of doubtful value." It is consoling that, as the subject of this criticism, I have the company of such eminent investigators as Jeffrey, East, Blakeslee, Sax, Brink and others. For, in referring to the pollen work of this list of investigators, and with which my own name is included, they state: "Grains were first studied and measured in the various media used by other writers: water, sugar solutions of different degrees of density, fuchsin, lactic acid. . . . The results with the several media were in general the same; but in all of them one is studying and comparing *transformed* pollen grains, not the true normally shaped grains."

When a dry pollen grain is moistened and expanded, admittedly it changes its shape. But very often it is in this condition when it leaves its anther. Ferguson and Coolidge admit that this is so even with petunia pollen on a rainy day, but after a short exposure to dry air it loses its turgidity and presumably becomes more normal. Beyond question such changes in volume and shape must always be ascertained, and the investigator must remain cognizant of them in making deductions, whichever condition he chooses to regard as normal. If the grain has three furrows, which is the commonest number, it generally changes upon being moistened, from ellipsoidal or cylindrical in form to globular or even oblately flattened. But with these changes a further *transformation* takes place. The furrows open. The opening of a pollen-grain furrow may be likened to the opening of the human eye; the furrow margins correspond to the lids, the furrow membrane to the whitish sclerotic coat, the germinal aperture with its papilla to the iris with its pupil. Just as it is more interesting and instructive to observe an eye that is open than one that is

³ Mohl, H. von. Ann. Sci. Nat. Ser. 2. 3: 148. 1835.

⁴ Ferguson, M. C., & Coolidge, E. B. Am. Jour. Bot. 19: 644. 1932.

closed, so it is more interesting and instructive to observe a pollen grain that is expanded with its furrows open than one that is collapsed with them closed.

METHODS

Methyl-green-glycerine-jelly. A small amount of pollen, about as much as can be picked up on the flat end of a tooth pick, or less, is placed on the center of a microscope slide, a drop of alcohol added and allowed to partly evaporate. A second and third or even fourth drop may be added if necessary. The alcohol spreads out as it evaporates and leaves the oily and resinous substances of the pollen deposited in a ring around the specimen. The oily ring is wiped off with cotton moistened with alcohol, and, before the specimen has had time to completely dry, a small drop of hot melted methyl-green-glycerine-jelly is added and the pollen stirred in with a needle and evenly distributed. During the process the jelly is kept hot by passing the slide over a small flame, heating it just enough to sting but not burn the knuckle which may be used to test its temperature. A number 0 cover glass, which has been passed several times through the flame while held vertically with the forceps, is then placed over the specimen, and the slide gently heated. If the amount of jelly has been judged correctly the cover will settle into position with the gelatin reaching its periphery just when the pressure of the cover begins to be taken up by the pollen grains. This amount must be learned by experience and accurately gauged because a smaller amount leaves the grains crushed or flattened by the cover, or the mount incompletely filled, and a larger amount causes the preparation to be too thick for use with oil-immersion lenses.

If naturally shed pollen is not available, satisfactory material can generally be obtained from herbarium specimens, providing they were quickly and completely dried. Often it is only necessary to tap the dry flowers over the slide or crush a few anthers on it. If pollen cannot be removed in this way, a few anthers, or with the Compositae, a few florets may be removed from the specimen and placed on the slide. These are then moistened with alcohol, followed by a drop of water and heated to boiling. The pollen may then be teased out and the anthers and other debris removed, leaving the pollen in the water. The water is then drawn off with cotton or filter paper and the jelly added as before.

The glycerine jelly is prepared according to the method of Brandt (Lee, *Microtomist's Vade Mecum*, 7th Ed. p. 242), which is as follows. Soak some gelatin for two or three hours in cold water, pour off the superfluous water and heat until melted. To one part of this add one and one half parts of glycerine and, while still hot, filter through spun

glass pressed into the lower part of a heated funnel. Add two or three per cent phenol. Still keeping the mixture hot and fluid add, drop by drop, a saturated solution of methyl green in fifty per cent alcohol, until the glycerine jelly becomes fully as dark as green ink.

The relative proportions of glycerine and water are so balanced in this medium that the majority of pollen grains when placed in it are fully but rarely over expanded, and they never do burst and extrude their contents as is usually the case with ordinary aqueous media.

ATMOSPHERIC POLLEN SLIDES

The same medium is the best, in my experience, for catching atmospheric pollen and making pollen counts and identifications. To do this, a small drop of melted methyl-green-glycerine jelly is placed on a slide, spread out to occupy an area about equal to and of the same shape as the cover glass which is to be used in finishing the mount. The slide is exposed in a horizontal position protected from rain and sun by a shelter raised at least four inches above it. After twenty-four or forty-eight hours the slide is brought into the laboratory and examined with a hand lens, and any extraneous material like soot or sand which, if present, might prevent the cover glass from fitting into place, is removed. The slide is then heated, controlling the temperature with the knuckle as before, until any excess moisture which may have accumulated during the exposure, is driven off. It is then covered with a number 0 cover glass.

EXAMINATION OF DRY POLLEN

When it is desired to discover the unexpanded shapes of pollen, it may be observed in dry air with or without a cover glass. Such observations are also useful in determining the amount of oil naturally occurring on the surface of the grains, and as a check against the method given below; but under these conditions magnifications over two hundred times can scarcely be used to advantage. Nevertheless, even at this magnification the shapes of the grains can be learned and something of the mechanical action of their organs of volume-change-accommodation. If, however, a detailed examination of the grains in their unexpanded condition is desired, they must be stained and brought into a medium of suitable refractive index. This may be done as follows:

ANALINE OIL GENTIAN VIOLET METHOD

Place the pollen on the slide as before and add two or three drops of aniline oil which has been tinted with gentian violet only to a pale purple color. Heat gently over the flame, controlling the temperature with the

knuckle as before, until the grains become deeply stained. Allow the slide to cool to room temperature, draw off the excess oil with filter paper, wash by repeatedly adding xylol and drawing it off until all the oil and unabsorbed dye have been removed; then add a drop of Canada balsam and cover. This presents the grains unexpanded but brilliantly stained, and in a medium eminently suited for observation with high-power oil immersion lenses.

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The growth of *Rhododendron ponticum* in sand cultures¹

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In a study of the mineral nutrition of a plant, there are many factors which must be considered, for the intake of the nutritive elements involves complex chemical and physical processes. Much is already known concerning the nutrition of some plants, such as wheat, soybean, alfalfa and other agricultural crops, under definite experimental conditions. From a review of the literature on the subject of mineral nutrition, it is at once apparent that there is still a great deal to be learned regarding the response of other groups of plants to the mineral elements which are essential to growth.

The large group of plants usually classified as "ornamentals" serves as a typical illustration of the great number and diversity of the species to which little attention has been given from the standpoint of a systematic study of the mineral requirements of plants of such great economic value. It has been only within recent years that this large class has been considered as a field for the scientific investigation of problems in plant nutrition, and this attention has been forced largely by the rapidly growing commercial importance of this vast group of plants.

The data presented in the following pages deal with an important member of this large group. They are the result of an experimental study to determine the mineral requirements for good growth and development, from seed, of *Rhododendron ponticum* L. under experimental conditions carefully controlled, in so far as this is possible, with respect to the media in which the plants were grown.

It is recognized that it is not possible to determine the nutrient requirements of a plant growing in the soil, because of the complexity of such a medium which cannot be controlled or varied at will with any degree of satisfaction or accuracy, owing to the numerous unknown chemical and physical factors involved. Because of this handicap, sand was used as the substratum to which the elements required for growth were added in solution form. Solution cultures serve as the fundamental starting point in the scientific investigation of the mineral nutrition of any group of plants. Furthermore, by means of some adequate system of continuous flow at a constant rate, such as has been developed by Trelease and Livingston (1922), by Anderssen (1926), by Johnston (1927), or by Shive and Stahl (1927), the mineral constituents of a culture solution bathing the roots of an actively growing plant, while they cannot be held at an absolutely constant level, can be maintained indefinitely without any very pro-

¹ Journal Series paper of the New Jersey Agricultural Experiment Station, Department of Plant Physiology.

nounced variations from the original salt or ionic proportions due to the absorption activities of the plant.

The studies here reported mark the beginning of a series of investigations dealing with problems concerned in the nutrition of *Rhododendron ponticum*, a member of the family Ericaceae. They are the response to many inquiries for fundamental information concerning the nutrition and growth of this splendid ornamental which, it appears, is difficult to grow successfully when used as a subject in landscape gardening under conditions favorable for the growth of ornamentals of other families. It was primarily the purpose of this investigation to determine whether culture solutions, such as are known to produce excellent growth of plants belonging to the general class of non-woody agricultural species, would produce similar responses in this woody perennial. Also it was proposed to investigate the properties and possibilities of certain salt combinations in the development of this species, and to make a comparative study of the plants grown by the solution culture method with those produced by the usual commercial practices.

EXPERIMENTAL MATERIALS AND METHODS

The culture solutions. In the preparation of culture solutions the salts used were Merck's Blue Label reagents and Eimer and Amend's chemicals of tested purity. In the preparation of stock solutions the following salts were regularly used: mono-potassium phosphate, magnesium sulphate with its usual seven molecules of water of hydration, ammonium sulphate, and calcium nitrate with four molecules of water. The original stock solutions were made up in large quantities and stored separately in five-gallon carboys. These solutions were made up in 0.5 molar concentration. The distilled water used in this work was produced by a "Barnstead" still and stored in five-gallon carboys similar to those used for the stock solutions. The culture solutions were prepared from these concentrated stocks.

In order to vary the salt proportions of the culture solutions by definite increments and still hold the total osmotic concentration of the solutions at a constant level, recourse was taken to the plan adopted by Tottingham (1914). The twenty culture solutions here employed were chosen from the complete series of eighty-four solutions used by Tottingham, with the modification as proposed by Jones and Shive (1921), of substituting ammonium sulphate for potassium nitrate in equivalent partial osmotic concentration. Thus the solutions contained nitrogen in the two forms NH_4 and NO_3 . This series of 4-salt solutions was chosen for investigation with the rhododendron on the basis of previous work by Stahl and Shive (1933), Naftel (1931), Jones and Shive (1921), and Tiedjens and

Robbins (1931) who have shown that NH_4 -nitrogen when present in the growth medium plays a very important part in the early activities and development of certain agricultural species, and also that, in general, a growth medium containing nitrogen in the two forms in the proper proportions is more efficient than one containing either of these forms alone, other things being equal.

For ease of reference, table 1 gives the solution numbers (column two) of the twenty representative solutions selected from the Tottingham series

TABLE 1
Partial volume-molecular concentrations of mono-potassium phosphate, calcium nitrate, magnesium sulphate and ammonium sulphate in the solutions employed

CULTURE NO.	SOLUTION NUMBER	PARTIAL VOLUME-MOLECULAR CONCENTRATIONS ^a			
		KH_2PO_4	$\text{Ca}(\text{NO}_3)_2$	MgSO_4	$(\text{NH}_4)_2\text{SO}_4$
1	T ₁ R ₁ C ₁	0.00211	0.00146	0.01659	0.0014
2		0.00211	0.00438	0.01185	0.0014
3		0.00211	0.00730	0.00711	0.0014
4	R ₄ C ₁	0.00211	0.01022	0.00237	0.0014
5		0.00211	0.00146	0.01185	0.0042
6		0.00211	0.00438	0.00711	0.0042
7	R ₆ C ₁	0.00211	0.00730	0.00237	0.0042
8		0.00211	0.00146	0.00711	0.0070
9		0.00211	0.00438	0.00237	0.0070
10	T ₃ R ₁ C ₁	0.00211	0.00146	0.00237	0.0098
11		0.00633	0.00146	0.01185	0.0014
12		0.00633	0.00438	0.00711	0.0014
13	R ₃ C ₁	0.00633	0.00730	0.00237	0.0014
14		0.00633	0.00146	0.00711	0.0042
15		0.00633	0.00438	0.00237	0.0042
16	T ₅ R ₁ C ₁	0.00633	0.00146	0.00237	0.0070
17		0.01055	0.00146	0.00711	0.0014
18		0.01055	0.00438	0.00237	0.0014
19	T ₇ R ₁ C ₁	0.01055	0.00146	0.00237	0.0042
20		0.01477	0.00146	0.00237	0.0014

^a Osmotic concentration of each solution = 1 atmosphere.

of 84. These numbers refer to the position which the solutions and cultures occupy in the four-coordinate scheme employed by Tottingham to represent the series in diagram. This table also shows the partial volume-molecular concentrations (gram-molecules per liter of solution) of the salts as they were used. The total osmotic concentration of each solution was calculated to give approximately one atmosphere of possible osmotic pressure. Ferrous sulphate as the source of iron for the plants was added to the culture solutions in aqueous solution from stock freshly prepared each time just before being used. Boron as boric acid and manganese as manganous sulphate were added in concentration equivalent to 0.5 p.p.m. of each to every culture solution.

The sand and culture vessels. The white quartz sand which was used

as the substratum with the rhododendron cultures was prepared by washing with a heavy stream of tap water introduced at the bottom of a large container and then allowed to filter up through the sand, the surplus water flowing off over the top of the container. This washing was continued until the overflow water appeared perfectly clear and free of colloidal matter. The surplus tap water was drained off and the sand was then flushed several times with distilled water to remove the tap water retained by the sand.

Three-gallon glazed stoneware percolators were used as culture vessels. These vessels have a sloping, curved bottom with a 2.5 cm. hole in the center. A small watch glass placed over the hole prevents the sand from escaping but still permits free drainage. The vessels were filled with the washed sand to within 1 cm. from the top, and were then ready to receive the plants.

The plants and their treatment. The species chosen for this investigation, *Rhododendron ponticum*, is a native of Spain, Portugal and Asia Minor, and is not entirely hardy in this region. Nevertheless, it is very extensively used by nurserymen as an understock upon which most of the common hybrid varieties of rhododendron are grafted. This preference for *Rhododendron ponticum* as an understock is due, undoubtedly, to the fact that the plant is capable of developing an extensive and very efficient root system which reflects its vigor in the development of the hybrid grafts.

The plants used in these investigations were grown from seed in flats 50 cm. long, 35 cm. wide and 8 cm. deep, in a mixture of approximately equal proportions of leaf-mold, garden soil and sand. Because of the long time required for germination and the exceedingly slow growth of the young seedlings, it required from nine to ten months to produce plants large enough for convenient handling. These plants when transferred from the flats to the sand cultures for experimental treatment were about 2 cm. tall.

It cannot here be definitely stated what may have been the influence of this long period of development in the leaf-mold-soil-sand mixture upon the subsequent growth of the plants in the experimental cultures; therefore, in presenting the data this residual influence, whatever it may have been, will be disregarded, since it may reasonably be assumed that all the plants were similarly affected.

In order to obtain some quantitative data on this point, a comparative study was made of seedlings produced as above described and those grown from seed in pure quartz sand to a size sufficiently large for convenient handling in experimental cultures. For this purpose, seed obtained from Holland was sown on the surface of washed quartz sand in flats like

those containing the leaf-mold-soil-sand mixture. The larger grains of sand had previously been removed by sifting through a fine-meshed mosquito netting. During germination the flats were covered with glass to prevent the surface layer of sand from drying out. The flats were kept in a partially covered moist chamber at an average temperature of 16° – 18° C. After germination, the seedlings were supplied with a culture solution having a total osmotic concentration of 0.1 atmosphere and the following composition:

KH_2PO_4 , .00105 m.; $\text{Ca}(\text{NO}_3)_2$, .000146 m.; MgSO_4 , .00071 m.; and $(\text{NH}_4)_2\text{SO}_4$, .00014 m.

This solution has the same proportions of the four salts as solution $\text{T}_3\text{R}_1\text{C}_1$ given in table 1, but is only one-tenth as concentrated as that solution.

TABLE 2

Comparison of plants grown from seed germinated in a leaf-mold-soil-sand mixture with those from seed germinated in quartz sand

SEEDS GERMINATED IN	SEEDLINGS AT TIME OF TRANSPLANTING		PLANTS AT THE END OF THE EXPERIMENT		
	AGE AT TIME OF TRANSFER TO SAND CULTURES (MONTHS)	AVERAGE HEIGHT (CM.)	AGE (MONTHS)	PERIOD OF GROWTH IN SAND CULTURES (MONTHS)	AVERAGE HEIGHT (CM.)
Leaf-mold-soil- sand mixture	9	2	16	7	30
Sand	5	3	8	3	33

200 cc. of the solution was applied twice daily to the surface of the sand in the flats by means of a small hand sprayer.

The seedlings thus grown in sand and those grown in the leaf-mold-soil-sand mixture, when sufficiently large, were transplanted to the sand in the 3-gallon percolators and were grown for several months by precisely the same methods as were the plants in the three experimental series here to be described. The comparative data of these plants are given in table 2, which is self explanatory. The data show that the plants from seed germinated in the leaf-mold-soil-sand mixture and then grown for seven months by the sand culture method were not as large nor as vigorous at the age of sixteen months as were the plants from seed germinated in quartz sand, at the age of eight months, having been grown in sand cultures by the same methods for only three months. It is important to point out also that the seedlings developed in the leaf-mold-soil-sand mixture were subject to certain diseases which were totally absent from the seedlings developed in the quartz sand.

Three complete series of cultures were carried out in the greenhouse. These will be designated Series A, Series B, and Series C. Each series con-

sisted of 20 cultures, each culture of Series A and C having three plants per culture, and Series B having two plants per culture. Only one series was conducted during any one time period. Series A was carried out from November 1928 to May, 1929; Series B from June, 1930 to February, 1931; and Series C from June 1931 to January, 1932.

When the seedlings were transferred from the leaf-mold-soil-sand mixture to the sand in the 3-gallon percolators, the roots were carefully washed to remove adhering soil particles. The seedlings were then planted in the sand contained in the percolators at equal distances from the center and from each other. The seedlings were selected from large numbers, and care was exercised to choose only those which were as nearly alike as could be determined by observation, in size, vigor, and general appearance.

In order to avoid pronounced changes either in salt concentration or salt proportions of the culture solutions applied to the sand, the solutions were continuously renewed at constant rates by the method of continuous flow described by Shive and Stahl (1927). The continuous flow was maintained at a rate of approximately one liter of solution every 24 hours for each culture. The solution was allowed to drip on a watch glass placed on the surface of the sand in the center of the pot. It then percolated through the sand and dripped from the hole in the bottom of the pot.

Once each week the cultures were thoroughly flushed with distilled water, the purpose of which was to remove any accumulation of salts which might have formed at the surface of the sand due to evaporation. The cultures were allowed to drain for several minutes and the solution renewal by continuous flow was started immediately. Once each week also, the surface layers of sand in each pot were thoroughly loosened by stirring to a depth of one to two centimeters with a pointed glass rod. This prevented excessive evaporation from the surface, aided aeration of the cultures, and practically inhibited the growth of green algae on the surface of the sand.

During the growth period of each series, observations were made of the general character of the development of the plants, and any unusual phenomena or pathological conditions were noted. At the termination of each series, the plants were cut at the surface of the sand. Measurements were made of the height of the stem above the sand and the diameter of the stems at the base. The leaves were separated from the stems and blue-prints were made of all the leaves of each plant. From these prints the total leaf area of each plant was obtained by tracing the leaf outline with a compensating planimeter. The stems and leaves were then cut into small pieces to facilitate drying and their dry weights obtained in the usual way.

EXPERIMENTAL RESULTS

Dry weights and leaf areas. Since green weight yields, dry weight yields, leaf areas, stem diameters and height of stems were obtained at the termination of each of the three series, five sets of growth measurements are available for each culture. However, only two sets of these measurements (dry weights and leaf areas) will here be presented, since the dry weight yields followed by leaf areas may safely be regarded as the most reliable of the five criteria, and since the remaining three, in a general way, show the same relationships as do these two. When dry weights are taken as a standard and the correlation coefficients of the others are calculated according to the formulae as given by Yule (1922), the leaf area records show the highest correlation ratio ($1.00 \pm .00007$). The remaining records in the descending order of the value of their correlation coefficients are green weights ($1.00 \pm .0027$), stem heights ($.964 \pm .0045$), and stem diameters ($.860 \pm .016$). The numerical data of dry weight yields and of leaf areas for the plants of each of the three series are presented in table 3. The data in the columns marked 'average' are the values obtained by averaging corresponding data from the three series, each average value thereby involving three cultures and eight plants. Each value in the table is relative to the corresponding value of culture 1, taken as 100. The actual yield values for this culture are given in parentheses, in grams for dry weights, and in square centimeters for leaf areas. The actual yield measurements for any culture may be obtained by multiplying its relative value by the corresponding actual value given in parentheses for culture 1.

The response of the rhododendron plants to the different salt proportions of various solutions to which they were exposed in the sand cultures, will here be considered with reference to the range in the proportions of each salt within which high average quantitative growth measurements for this species were obtained. These ranges for high yields will be compared with the corresponding ranges for the entire series.

From the data of table 3, it will be observed that a fairly wide range of relative yield values of dry weights and leaf areas occurs within each series, which may be in a large measure, if not entirely, attributed to the variations in the relative salt proportions from culture to culture in the respective series. Since low and medium values hold little of interest or value in this connection, they will not be considered here.

The highest five average measurements of dry weight yields and leaf areas, and the salt proportions of the solutions which produced these, together with the ranges from the highest to the lowest of each set of values, have been brought together in table 4. For facility in making comparisons, the table also shows the maximum, minimum, and range values

of the partial volume-molecular salt concentrations and growth measurements for the entire series.

It is to be pointed out that the highest five yields in the three different series were not always produced by corresponding cultures, as is indicated by the data of table 3. Only one culture within the range of those pro-

TABLE 3

The relative values of the dry weights of tops and of leaf areas of plants grown in four-salt solutions, all having a total osmotic concentration of 1.0 atmosphere, but differing from each other in the proportion of the four salts

CULTURE NUMBER	RELATIVE GROWTH VALUES (AVERAGE PER PLANT)							
	DRY WEIGHT OF TOPS				LEAF AREAS			
	SERIES A	SERIES B	SERIES C	AVERAGE	SERIES A	SERIES B	SERIES C	AVERAGE
1	1.00 (5.49)	1.00 (26.8)	1.00 (15.7)	1.00 (16.0)	1.00 (685)	1.00 (1820)	1.00 (1264)	1.00 (1256)
2	0.73	1.26	0.73	0.91	0.80	1.20	0.76	0.92
3	0.76	1.66	0.63	1.02	0.74	1.60	0.63	0.99
4	0.72 ^a	1.26	0.65	0.88	0.82	1.17	0.66	0.88
5	1.07	1.63	1.38	1.36	1.10	1.37	1.26	1.24
6	0.82	1.66	1.22	1.23	0.78	1.37	1.12	1.09
7	1.09	1.08	0.59 ^a	0.92	1.02	1.09	0.53	1.05
8	0.94	1.10	0.84	0.96	0.97	1.13	0.91	0.99
9	1.31 ^a	1.82	1.13 ^a	1.42	1.10 ^a	1.62	1.08 ^a	1.27
10	0.85	1.35	1.01	1.07	0.97	1.37	1.09	1.14
11	1.18 ^a	0.84	1.32	1.11	1.22 ^a	0.92	1.25	1.13
12	0.90	1.82	1.00	1.24	0.78	1.56	0.98	1.11
13	0.63	1.47	0.94	1.01	0.67	1.34	0.86	0.96
14	0.93	1.51	1.40	1.28	0.96	1.54	1.41	1.30
15	0.88	1.71	0.91	1.17	0.86	1.57	0.89	1.11
16	0.83	1.45	1.02	1.10	0.87	1.44	1.06	1.12
17	1.07	1.39	1.04	1.17	0.96	1.50	1.10	1.19
18	0.77	1.43	0.94	1.05	0.76	1.38	0.86	1.00
19	0.88	1.70	0.96	1.18	0.81	1.65	1.02	1.19
20	0.96	1.47	1.03	1.15	1.05	1.41	1.04	1.17

^a Two plants per culture.

ducing high yields is common to the three series. This is culture 9. This lack of agreement between the cultures of the three series may be accounted for by the fact that only one series was conducted during any one experimental period. The three series were carried out during three different years and were not begun nor terminated at the same season of the year. Of course, it was not within the province of this investigation to evaluate the influence of seasonal change or environmental differences upon growth as related to the inorganic nutrition of the rhododendron.

Considering the average dry weight criterion, it will be observed from table 4 that the volume-molecular proportions of the four salts characterizing the culture solutions which produced high dry weight yields, without exception, are limited to certain ranges which are less extensive than the corresponding total ranges for the entire series. The range in the propor-

tions of KH_2PO_4 and $\text{Ca}(\text{NO}_3)_2$ which produced high yields are relatively narrow in comparison with the corresponding ranges for the entire series. The proportions of $(\text{NH}_4)_2\text{SO}_4$ and MgSO_4 show a relatively wide range within which high dry weight yields were produced.

The range in average dry weight values for the five cultures producing high yields is quite narrow, extending from 22.5 grams to 24.6 grams per

TABLE 4
Volume molecular salt proportions and ranges of these for the solutions which produced the highest five average measurements of dry weight and leaf areas

	CULTURE NUMBERS	PARTIAL VOLUME-MOLECULAR CONCENTRATIONS				AVERAGE GROWTH MEASUREMENTS PER PLANT	
		KH_2PO_4	$\text{Ca}(\text{NO}_3)_2$	MgSO_4	$(\text{NH}_4)_2\text{SO}_4$	DRY WEIGHT GMS	LEAF AREAS SQ. CM.
Cultures Producing Highest Five Dry Weight Yields	5	.00211	.00146	.01185	.0042	23.4	
	6	.00211	.00438	.00711	.0042	22.7	
	9	.00211	.00438	.00237	.0070	24.6	
	12	.00633	.00438	.00711	.0014	23.1	
	14	.00633	.00146	.00711	.0042	22.5	
	Range	.00422	.00292	.00948	.0056	2.1	
Cultures Producing Highest Five Yields of Leaf Area	5	.00211	.00146	.01185	.0042		1612
	9	.00211	.00438	.00237	.0070		1690
	14	.00633	.00146	.00711	.0042		1744
	17	.01055	.00146	.00711	.0014		1592
	19	.01055	.00146	.00237	.0042		1615
	Range	.00844	.00292	.00948	.0056		152
Entire series	Maximum	.01477	.01022	.01659	.0098	24.6	1744
	Minimum	.00211	.00146	.00237	.0014	14.7	1118
	Range	.01266	.00876	.01422	.0084	9.9	626

plant, with a range of 2.1. This indicates that the five culture solutions which produced the highest five average yields of dry plant material show nearly equal efficiency in producing good rhododendron plants under the experimental conditions here described.

Turning now to the criterion of average leaf areas, the data of table 4 show that the ranges in the molecular proportions of $\text{Ca}(\text{NO}_3)_2$, MgSO_4 and $(\text{NH}_4)_2\text{SO}_4$ in the solutions which produced the highest five average yields of leaf areas are identical with those of the solutions which produced the highest five average dry weight yields. While the molecular proportions of KH_2PO_4 in the cultures which produced high average yields of dry plant material show a relatively narrow range, those of the solutions corresponding to the highest five average leaf area measurements show a relatively wide range as compared with the total range for the entire series.

The range in the absolute average leaf areas for the cultures yielding the highest five measurements is quite narrow and bears approximately the same relation to the total range for the entire series as does the range in dry weights, for the five high yielding cultures, to the corresponding range for the entire series. Three cultures in the group of five which gave the highest average leaf area measurements are also in the group of five cultures which produced high average dry weight yields. These cultures are 5, 9, and 14, corresponding to the solution numbers in table 1.



Fig. 1. Plants in two cultures selected from the best five (left), and two selected from the poorest five (right) in series B at the termination of the experiment. Age of plants 16 months from seed.

It is to be emphasized that while the highest five average yields produced by the solutions of the series employed were much superior to the lowest five average yields, not a single set of salt proportions in the entire series failed to produce what might be regarded as fairly good plants. This is clearly indicated in figure 1, which shows photographs of two cultures selected from the best five in Series B and two selected from the poorest five, at the termination of the series. No pronounced injurious effects which could be traced directly to an unbalanced condition of salt proportions, appeared in any culture of the series. While the plants of some cultures were much smaller than those of others, as the data indicate, and were considerably retarded in development as compared with the plants which made optimum growth in the series, they were, nevertheless, healthy and vigorous plants. This is an indication that within certain limits *Rhododendron ponticum* is not particularly sensitive to variations in

salt proportions, so long as the extreme variations do not actually involve an absolute deficiency of an essential element.

From the data presented in table 4, it appears that the poor growth of rhododendron so often encountered in the field is probably not due to an unfavorable balance of the elements required in major quantities for growth, since the species is tolerant of a fairly wide range in the proportions of these elements. This evidence tends to indicate that there are other factors which are operative here. One of these factors, however, may still be nutritional in nature, as the retarded growth may be due to a deficiency of some one or more of the essential ions required in minor quantities for growth.

Apparent condition of plants. It is a matter of some interest to note, as already pointed out, that no combination of the salts employed produced what might be termed a severe pathological condition in the plants. During the course of the three series, however, five plants out of a total of 160 died, but this was due to originally diseased stock and not to any severe nutritional disturbance, inasmuch as the remaining plants in each of the cultures containing the originally injured one survived and made excellent growth.

While none of the experimental treatments resulted in pronounced injury, it was obvious that for the rhododendron some of the solutions were poorly balanced with respect to the proportions of the four constituent salts. The only obvious injury which appeared manifested itself in a chlorotic condition of the plants in several cultures. This chlorosis appeared at an early stage in the plants of corresponding cultures in each of the three series. These cultures were 3, 4, 7, and 13, each having relatively high proportions of calcium nitrate and low proportions of the three other salts. The chlorotic condition of the plants was readily traced to their inability to obtain and utilize efficiently the iron from the solutions supplied to these cultures. By maintaining relatively high concentrations of iron in the solutions, the chlorotic condition of the plants in three of the cultures completely disappeared. The plants in culture 4, however, in which the solution contained the maximum proportion of calcium nitrate and the minimum proportions of each of the other three salts, remained chlorotic throughout the growth period.

It is of interest to point out that although the solutions were continuously renewed, the roots of the slow-growing rhododendron produced considerable change in the reaction of the medium during the absorbing process. In table 5 are recorded the hydrogen-ion concentrations, expressed as pH, of the twenty culture solutions of Series B at different stages in the growth period after the roots of the plants had been in con-

tact with the solutions in the sand cultures for a definite interval of time.

In preparation for making pH determinations, each sand culture was flooded with distilled water and then allowed to drain until dripping from the hole in the bottom of the container ceased. This was done to remove as much as possible of the old solution from the sand and roots of the plants. New solution was then percolated through the sand for a period of 24 hours by the continuous flow method at the rate of one liter in 24 hours.

TABLE 5

Hydrogen-ion concentrations, expressed as pH, of the culture solutions and leachings from the cultures at various stages of growth

CULTURE NUMBER	HYDROGEN-ION CONCENTRATION, EXPRESSED AS pH			
	CULTURE SOLUTION (ORIGINAL)	LEACHINGS FROM CULTURES AFTER VARIOUS INTERVALS OF GROWTH		
		9 WEEKS	16 WEEKS	21 WEEKS
1	4.46	3.80	3.46	3.65
2	4.48	3.90	3.65	3.58
3	4.47	3.82	3.71	3.51
4	4.53	3.83	3.73	3.46
5	4.56	3.82	3.45	3.45
6	4.53	3.84	3.61	3.57
7	4.55	3.87	3.62	3.67
8	4.53	3.93	3.53	3.66
9	4.48	3.89	3.66	3.49
10	4.55	4.00	3.57	3.56
11	4.35	3.86	3.48	3.63
12	4.30	3.97	3.55	3.67
13	4.29	4.11	3.45	3.46
14	4.29	3.83	3.47	3.84
15	4.30	4.02	3.63	3.59
16	4.31	3.88	3.52	3.47
17	4.18	3.89	3.51	3.59
18	4.19	3.97	3.82	3.82
19	4.23	3.77	3.36	3.69
20	4.15	3.69	3.53	3.60

Samples of the drip from the opening in the bottom of each pot were then collected and the pH of the solutions determined electrometrically.

It will be observed that the solutions of the different cultures in the series are all rendered quite acid through differential absorption of essential ions, and indeed this condition appears to be necessary, under the conditions of these experiments, to avoid chlorosis in the plants due to an apparent deficiency of available iron. However, the rhododendron apparently absorbs and assimilates iron only with some difficulty, particularly from a medium the pH of which approaches the point of neutrality. It is here suggested that this may be a direct effect of relatively high pH values of the medium upon the absorbing and assimilating power of the plant, which may render the absorption and assimilation of iron by the rhododendron quite difficult, and may not be entirely the result of iron de-

ficiency due to precipitation from solution. This is given as a suggestion and not as a fact established by experimental evidence.

By special methods it has been possible to produce excellent rhododendron plants by the use of balanced solutions of the series here employed, at pH values considerably above the point of complete precipitation of inorganic iron, as established by the work of Patten and Mains (1920). This was accomplished as follows: Solution $T_5R_1C_1$ of the series was used as the culture medium. The pH of this solution was adjusted to 6.5-7.0 by the partial substitution of the di-basic potassium phosphate for the monobasic form. With this solution so adjusted, the plants were grown in sand cultures in precisely the same manner as were the plants of the regular series, except that the rate of continuous flow of the solution was somewhat higher, in order to avoid any pronounced reduction in pH of the solution through contact with the plant roots. Twice a week each of the cultures was flooded with one liter of distilled water and allowed to drain, to remove most of the solution from the sand and roots of the plants. 400 cc. of an aqueous solution of $FeSO_4$ (100 p.p.m. of iron) was then poured upon the sand in the culture. This was allowed to remain thirty minutes, after which the continuous flow method of renewal of culture solution was resumed.

With this modification in the cultural method, excellent rhododendron plants were grown without the appearance of chlorosis. Without this modification in the cultural method, the use of solutions at pH 6.0-7.0 resulted only in severely chlorotic plants and ultimately in the death of the plants. Thus, in the absence of the culture solution these plants were able to absorb, from a dilute aqueous solution of iron, and assimilate during the brief interval of thirty minutes, sufficient of this element to satisfy their requirements for normal growth and development. In the presence of the culture solution at pH 6.0-7.0 and with an adequate concentration of iron in the medium, the plants failed utterly to absorb or to assimilate the necessary supply of this element for normal growth and development.

Observations on older rhododendron plants grown in sand cultures. In the time period during which the three experimental series above de-



Fig. 2. Plant on the right grown in soil; age two years, height 0.76 meters. Plants on the left grown in sand culture; age two years, height 2.4 meters.

scribed were conducted, certain observations were made on older rhododendron plants which had been grown continuously in sand cultures by the method here described. Seedlings from seed germinated in sand in February, 1929 were transferred in November of the same year to the sand in three-gallon percolators, like those employed in the regular series. Here they were grown in the greenhouse in sand continuously supplied with solution $T_5R_1C_1$ by the continuous flow method until they bloomed in July 1931 at the age of two and one-half years. These plants again bloomed in February 1932, at the age of three years. By a successive development of the individual florets in the clusters, this second bloom continued over a period of seven weeks.

In figure 2 are shown photographs of two of these plants at the age of nearly two years, compared with one of the same age grown in a good soil—(sand-leaf-mold-mixture) side by side with the two grown in sand cultures. These three plants were transplanted as seedlings at the age of five months, from the same seed bed of sand at the same time. The plants grown in sand cultures continuously supplied with a culture solution averaged 2.4 meters in height; those grown in the soil-sand-leaf-mold-mixture showed an average height of 0.76 meters.

In May 1931, six plants from this same group which had been grown by the sand culture method, were removed from the sand cultures in which they had been growing, the surplus sand was shaken from their roots, and in this condition they were transplanted out-of-doors in ordinary garden soil. When transplanted into the open they averaged nearly one meter in height. Each of these six plants not only survived the transplanting in excellent condition, but also made very good growth during the summer and fall months, in spite of, or perhaps in a stricter sense, because of the rapid forcing by means of the sand culture treatment which they had received during the first 15 months of their growth. With slight protection all of these plants survived the winter out-of-doors in excellent condition, although this species is not considered entirely hardy in this latitude. Some of these plants developed excellent flower buds and bloomed during the season of 1932, at the age of less than two and one-half years from seed, and produced mature seeds in the fall of 1932.

The ability of these plants to withstand the shock of transplanting and to endure the rigors of the hot summer months in an exposed position in the open, without serious check to growth and development, may be attributed to the remarkable root systems which the plants produce under the influence of the sand culture method with continuous solution flow. The plants under these growing conditions produce very elaborate systems of vigorous, finely-branched, fibrous roots, which expose to the

growth medium unusually extensive absorbing surfaces. These roots provide most efficient absorbing systems, and their efficiency is abundantly reflected in the vigor of top growth, as may be observed from figure 3, which shows a photograph of an average plant at the age of two years and eight months.

During the entire period of development, the seedlings employed in these experiments, grown from seeds germinated in sand, remained free from the common diseases of rhododendrons, although no special precautions were taken to prevent disease of any kind.



Fig. 3. Average plant grown in sand culture with continuous solution flow. Age two years eight months from seed.

It is thus clear that the sand culture method of seed germination and early growth of the seedlings of this species offers not only certain advantages in the development of experimental plants for purposes of investigation, but also advantages which may be usefully applied in commercial production.

SUMMARY

Seedlings of *Rhododendron ponticum* were grown in sand cultures continuously supplied with culture solutions by a method of continuous solution renewal at constant rates. Twenty different sets of salt proportions of the four component salts KH_2PO_4 , $\text{Ca}(\text{NO}_3)_2$, MgSO_4 , and $(\text{NH}_4)_2\text{SO}_4$ were simultaneously tested, all at a total osmotic concentration of one atmosphere. The results may be briefly summarized as follows:—

1. Volume-molecular proportions of the four salts characterizing the five solutions which produced the plants yielding the highest five average measurements of dry weight in a series of twenty cultures, are limited to certain ranges which are considerably less extensive than the corresponding total ranges for the entire series.

2. For these five solutions, ranges in the proportions of KH_2PO_4 and $\text{Ca}(\text{NO}_3)_2$ are relatively narrow, while those of MgSO_4 and $(\text{NH}_4)_2\text{SO}_4$ are relatively wide in comparison with the corresponding ranges for the entire series.

3. These five solutions show nearly equal efficiency in producing good rhododendron plants.

4. Within certain limits, *Rhododendron ponticum* is not particularly sensitive to variations in salt proportions, so long as these do not actually involve an absolute deficiency of one of the essential elements. Not a single set of salt proportions in a series of twenty, produced what might be regarded as a severe pathological condition in the plants.

5. The sand culture method of seed germination and early growth of seedlings of *Rhododendron ponticum* offers advantages which may be usefully applied in the development of experimental plants and in commercial production.

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A revision of the section *Gymnocaulis* of the genus *Orobanche*

DAISY M. ACHEY

(WITH FIFTEEN TEXT FIGURES)

This revision has been done under the direction of Dr. Philip A. Munz of Pomona College, to whom I hereby acknowledge my deep indebtedness. I wish also to express my appreciation to those in charge of the following herbaria from which material was borrowed: Gray Herbarium of Harvard University (G), University of California (C), Missouri Botanical Garden (M), United States National Herbarium (U. S.), Pomona College Herbarium (P). The abbreviation given with each name above is used in citing specimens. My gratitude is also due to Mr. W. N. Suksdorf of Bingen, Washington for his kindness in lending type material of the species he has described.

As here treated the section *Gymnocaulis* includes the same plants as in Beck's recent revision of the genus *Orobanche* (Das Pflanzenreich **4**²⁶¹: 46. 1930). It consists entirely of North American plants. But after careful study of much herbarium material and after making dozens of camera lucida drawings of the flowers, I would treat somewhat differently the taxonomy of the plants in this section and would recognize but two species, *O. uniflora* and *O. fasciculata*, with their several varieties. The diagnostic characters for these species are quite definite and the two are easily separated from each other. But an attempt at the classification of the species into varieties is not so satisfactory. In any given character studied there is a gradation from one extreme to the other. For example, there is a continuous series of plants from those with glabrous to those with densely pubescent anthers. The color, size, and shape of the floral parts were found to be as variable as the pubescence on the anthers. However, the differences in the plants of a given species were too marked to make it seem advisable to place them all together. I have separated them, therefore, on the basis of the most constant characters observed, while at the same time recognizing the high degree of intergradation between the varieties.

The divisions were more definite in the *uniflora* than in the *fasciculata* group. In *O. uniflora*, I found considerable intergradation between the three western varieties: *purpurea*, *Sedi*, and *minuta*. But these three separated nicely, both morphologically and geographically, from the two eastern varieties. Suksdorf (Allg. Bot. Zeitsch. **12**: 27. 1906) would recognize *Aphyllon inundatum* as a fourth western entity. But there seems to me to be more variation within the variety *Sedi* than between the types of *Sedi*

Ciliation on corolla lobes ca. 0.5 mm. long. In Newfoundland.

1b. *O. uniflora* var. *terrae-novae*

Calyx lobes about twice as long as tube, narrowly subulate from a broad base. Plants from Rocky Mts. and West.

Anthers usually pubescent; corolla 22–30 mm. long, tube 5–8 mm. wide at the throat. 1c. *O. uniflora* var. *purpurea*

Anthers glabrous; corolla usually 15–22 mm. long, tube 3–5 mm. wide at the throat.

Corolla purple; parasitic on Saxifragaceae. 1d. *O. uniflora* var. *minuta*

Corolla yellow or tinted with lavender; parasitic on *Sedum* or Compositae. .

1e. *O. uniflora* var. *Sedi*

1a. *O. uniflora* L. var. *typica*, n. nom.

O. uniflora L., l.c.; G. Beck, Mon. Orob. 74: 1890, in part; *Anoplanthus uniflorus* Endlicher, Gen. Pl. 727. 1836–40; *Aphyllon uniflorum* Gray, Man. Bot. ed. 1, 290. 1848; Syn. Fl. 2¹: 312. 1878; *Thalesia uniflora* Britton, Mem. Torrey Club 5: 298. 1894; *O. biflora* Nutt. Gen. N. Am. 2: 59. 1818; *Phelipaea biflora* Sprengel, Syst. 2: 818. 1825; *Anoplon biflorum* G. Don, Syst. 4¹: 634. 1838.

Pedicels usually paired, 6–15 cm. long, 0.5 to 0.75 mm. thick; corolla 2–3 cm. long, yellowish, often with lavender lines in the throat and azure on the margins; the lobes obovate, 3–5 mm. long, strongly ciliated on margins; throat scarcely enlarged, tube slightly constricted in upper part; anthers only slightly pubescent.

Type locality, "Habitat in Virginia." Ranging throughout the Atlantic States and west to the Rocky Mt. States. Representative material, MACKINAW ISLAND: Arch Rock, *Wright* in 1915 (G). ONTARIO: Agawa River, *Pease* 18957 (G). MAINE: Orono, *Fernald* 2438 (G); Westbrook, *Ricker* 54 (U. S.). NEW HAMPSHIRE: Groton, *Steele* in 1882 (P). VERMONT: Rutland, *Eggleston* 2589 (M). MASSACHUSETTS: Cummington, *Williams* in 1907 (G); Cambridge, *Tuckerman* 814 (U. S.). CONNECTICUT: Norwich, *Linnsden* in 1884 (C). NEW YORK: Peaked Mts., Washington Co., *Ann* in 1900 (P); Ithaca, *Munz* 366 (P); Brooklyn, *Hicks* in 1886 (G). RHODE ISLAND: Johnstown, *Collins* in 1890 (G, U. S.). NEW JERSEY: Milltown, *MacKenzie* 3048 (M). PENNSYLVANIA: Lancaster, *Small* in 1890 (M, U. S.); Sunneyton, *Smith* in 1905 (C). MARYLAND: Baltimore, *Steitz* in 1894 (U. S.); College Park, *Pond* in 1901 (G). DISTRICT OF COLUMBIA: WASHINGTON, *Steele* in 1897 (G); Seven Locks, *Steele* in 1898 (U. S.). VIRGINIA: Charlestown, *Pringle* in 1876 (P). WEST VIRGINIA: Upshur, *Nutter* in 1897 (M, U. S.). NORTH CAROLINA: Asheville, *McCarthy* in 1888 (U. S.). SOUTH CAROLINA: Keowee, *House* 1896 (U. S.). FLORIDA: Jacksonville, *Smith* 445 (U. S.). MISSISSIPPI: Tchula, *Woodsen & Anderson* 1519 (M). KENTUCKY: Natural Bridge, *McFarland* 76 (M). TENNESSEE: Knoxville, *Ruth* in 1898 (M, U. S.). OHIO: Brady Lake, *Portage Co.*, *Webb* in 1923 (G). ILLINOIS: Park Ridge, *Walker* in 1905 (U. S.). MICHIGAN: Whitmore Lake, Washtenaw Co., *Chandler* in 1915 (U. S.). IOWA: Ames, *Stewart* in 1893 (M). NEBRASKA: Lincoln, *Williams* in 1886 (U. S.). KANSAS: Prairie, Riley Co., *Hansen* 1007 (G, M, U. S.). MISSOURI: Courtney, *Bush* 7100 (C, G, M, U. S.); St. Louis, *Engelmann* in 1842 (M). OKLAHOMA: Leflore Co., *Blakley* 3436 (G). ARKANSAS: Far-

mington, *Palmer 24758* (M). MONTANA: Belt River, *Williams 239* (C); Camp 13, Southern Montana, *Rose 247* (U. S.).

The two collections of var. *typica* from Montana represent an exception to the usual absence of this variety in the Rocky Mountain States.

1b. *Orobanche uniflora* L. var. *terrae-novae* (Fernald), n. comb.

Orobanche terrae-novae Fernald, *Rhodora* 28: 235. 1926.

Very similar to var. *typica*. Peduncles about 1 mm. thick; corolla lobes oblong, 5-7 mm. long.

Type locality, Bard Harbor, St. John Bay, Newfoundland. Ranging throughout Newfoundland. Material seen—NEWFOUNDLAND: Bard Harbor, *Wiegand et al. 29049*, type specimen, (G); Stanleyville, *Fernald et al. 2014* (G); Killdevil, *Fernald et al. 2015* (G); Hannah's Head, *Fernald & Long 2016* (G); St. John Island, *Fernald et al. 29050* (G); Burnt Cape, *Fernald & Long 29051* (G); Coal River, *Waghorne* in 1886 (G); Grand Falls, *Fernald & Wiegand 6211* (G); Birchy Cove, *Fernald & Wiegand 4018* (G); Doctor Hill, *Fernald & Long 29052* (G); Harbor Hill, *Fernald & Long 29053* (G); Penguin Hill, *Fernald et al. 2013* (G).

Fernald gives specific rank to *O. terrae-novae*. But he suggests that "it is merely a geographic variety," and my observations tend to verify this statement. The characters separating the two groups seem too insignificant to warrant giving more than varietal rank to *O. terrae-novae*. Fernald calls attention to two linear yellow lines on the throat. But Nuttall gives this (Gen. N. Am. 2: 59. 1818) as a character of *O. biflora* (placed here as a synonym of var. *typica*). According to Fernald *O. terrae-novae* is odorless while var. *typica* is fragrant.

An example of the similarity between the two groups may be seen in the following two sheets: South Carolina, Keowee, *House 1896* (U. S.) and Newfoundland, Birchy Cove, *Fernald & Wiegand 4018* (G). In both these sheets the length of the corolla lobes ranges from 3 to 5 mm. In the Newfoundland one, as is usual in *terrae-novae*, the ciliation tends to be longer and the pedicels thicker than in *typica*. However the lobes in the Newfoundland plant are less oblong than those of Carolina, although they should be more so. Another example of *typica* with long, oblong lobes is a specimen from Arkansas: Hotsprings, *Palmer 24506* (M.).

The following specimens from Quebec were annotated as *O. terrae-novae* by Fernald: Renard River, *Victorin & Germain 27906* (G); Chicotte River, *Victorin & Germain 27908* (G); Carbeaux, *Rousseau 26652* (G). The other specimens from Quebec he leaves as *Orobanche uniflora*: Rimouski Co., *Fernald & Collins 1154* (G); River Juniter, *Victorin & Germain 25459* (G); Stanstead, *Knowlton* in 1924 (C). But they all seem to be intergrades between *terrae-novae* and *typica*. The corolla lobes tend to be obovate and the ciliation short as in *typica*. But the pedicels are thick as in *terrae-novae*. The length of the lobes ranges between that of the two varieties, i.e. from 3 to 7 mm.

1c. *Orobanche uniflora* L. var. *purpurea* (Heller), n. comb.

Thalesia purpurea Heller, Bull. Torrey Club 24: 313. 1897; *Orobanche porphyrantha* Beck, Pflanzenreich 4²⁶¹: 49. 1930.

Pedicels 3 to 10 cm. long; corolla usually deep purple, constricted at base of tube and becoming 5 to 8 mm. wide at throat.

Type locality, Lewiston, near mouth of Potlach, Idaho. Ranging from British Columbia through Washington, Oregon and Idaho to southern California. Representative material—BRITISH COLUMBIA: Jardo, *Shaw* 691 (U. S.). WASHINGTON: Tacoma, *Rensselaer* in 1894 (G); Blue Mts., *Horner* 403 (U. S.); Yakima region of Cascades, *Brandegee* 14197 (M); Cheney, *Tucker* in 1890 (G); Wenatchee Mts., *Elmer* 463 (G); Bingen, *Suksdorf* 2323 (C, G, M, U. S.); Ellensburg, *Whited* 327 (U. S.); Wawawai, *Elmer* in June 1897 (M). OREGON: Hood River Co., *Henderson* 543 (M); The Dalles, Wasco Co., *Sheldon* S. 10209 (G, M, P, U. S.); Blue Mts., *Henderson* 5416 (G); Pendleton, Umatilla Co., *Gale* 529 (M); Mt. Emily, *Cusick* 2396 (C, G, M, P, U. S.); Rock Creek, *Leiberg* 76 (G, M, U. S.). CALIFORNIA: Yreka, *Smith* 638 (G, U. S.); Mendocino Co., *Bolander* 4677 (C, G, U. S.); Donner Lake, *Sonne* in 1886 (C); Little Chico Canyon, *Austin* in 1897 (U. S.); Hupa, *Manning* 96 (C); Mts. north of San Francisco, *Rattan* 54 (G); Grahams, Humboldt Co., *Blasdale* in 1896 (C); Sierra Mts., *Davidson* in 1885 (P); Musser Hill, *Gale* 354 (P); Lake Tahoe, *Chestnut & Drew* in 1890 (C); Santa Cruz Mts., *Pendleton* 278 (U. S.); Long Valley, *Brewer* 4677 (U. S.); Tamarack Lake, *Essig* in 1928 (C). IDAHO: Coeur d'Alene, *Rust* 114 (U. S.); Lewiston, Nez Perces Co., *Heller* 3099, type collection, (C, M, U. S.); Squaw Creek, Boise Co., *Macbride* 813 (C, G, M, P, U. S.); Middle Valley, *Jones* in 1900 (P).

Some plants from Texas (without locality), *Lindheimer* 489 (M, U. S.), have not been cited with this group for they might belong to the var. *typica*. The calyx lobes are lanceolate as in var. *typica*, but the plants are darker and less delicate than in *typica*. They also do not have the purple margin on the corolla lobes which is characteristic of var. *typica*. There is another collection from the immediate range of var. *purpurea* which resembles the ones from Texas: CALIFORNIA, Comptche, Mendocino Co., *Walker* 368 (C). I am placing them all as doubtful specimens of var. *purpurea*, for they probably belong more nearly to this group than to any other variety of *O. uniflora*. Their long pedicels (15–20 cm.) and pubescent anthers would separate them from var. *Sedi* and var. *minuta*.

In his recent revision (Pflanzenreich 4²⁶¹: 49. 1930) Beck keeps *O. porphyrantha* (*purpurea*) as a species distinct from *O. uniflora*. The results of my work in the group would lead me to place it as only a variety of *O. uniflora*. Beck has reduced *minuta* to a variety and var. *Sedi* to a form of *O. uniflora*. I do not find that *purpurea* differs more from *typica* than either *minuta* or *Sedi* does. It is true that var. *purpurea* is darker and its corolla tube tends to be broader than in var. *typica*. But in var. *minuta* the corolla lobes are less spreading and the plant is smaller and darker than in var. *typica*. In var. *Sedi* the lobes are truncate or oblong, not spreading and the plant is usually of smaller size, thus making it as distinct an entity from var. *typica* as var. *purpurea* is. Some specimens of var. *purpurea* are quite light while some of var. *typica* are tinged with considerable purple. The

breadth of the corolla lobes is more or less variable in both groups. For these reasons I am considering *purpurea*, as well as *Sedi* and *minuta*, as varieties of *O. uniflora*.

There is a high degree of intergradation between var. *Sedi* and var. *purpurea*. Their affinity is especially shown in the plants from Idaho which have a tendency to have lighter corollas and less pubescent anthers than most others in the var. *purpurea*. I have seen three sheets of the type collection; the one from the Missouri Botanical Garden has glabrous anthers as in var. *Sedi*. Another intermediate form is from Vancouver Island, Victoria, *Macoun* 750 (M). The corolla is dark purple and shaped like var. *purpurea*, but the anthers are glabrous.

1d. *Orobanche uniflora* L. var. *minuta* (Suksdorf) G. Beck, Pflanzenreich **4**²⁶¹: 49. 1930.

Aphyllon minutum Suksdorf, Deutsch. Bot. Monatsschr. **18**: 155. 1900; *Thalesia minuta* Rydb. Bull. Torrey Club **36**: 693. 1909.

Pedicels 2–7 cm. long; corolla strongly curved, usually deep purple, tube 4–5 mm. wide at the throat, lobes rounded.

Type locality, Bingen, Klickitat Co., Washington. Ranging from British Columbia through Washington and Oregon to Southern California. Material seen—BRITISH COLUMBIA: Victoria, *Macoun* 88173 (M); Vancouver Island, Ford Bay, *Carter* in 1918 (G); Mt. Finlayson, *Carter* in 1918 (G); Selkirk Mts., *Butlers & Holway* 268 (G); Trail, *Macoun* 67881 (C). WASHINGTON: Pullman, *Elmer* 43 (P), *Piper* in 1894 (M); Bingen, *Suksdorf* 2345 (C, U. S., Suksdorf); Almota, *Piper* 1809 (G, M). OREGON: The Dalles, *Lunell* in 1903 (G); Elk Rock, *Nelson* 1268 (G); Selma, *Henderson* 6008 (M, U. S.); Grants Pass, *Piper* in 1921 (G); Wimer, Jackson Co., *Hammond* 320 A, May 22, 1893 (M, U. S.). CALIFORNIA: Egg Lake, Modoc Co., *Baker & Nutting* in 1894 (C); Shasta Valley, *Buller* 730 (C, P); Fisher's Cabin, Calaveras Co., *Hansen* 246 (M, P); Mokelumne Hill, Calaveras Co., *Blaisdell*, (G); Panoche Pass, San Benito Co., *Abrams & Borthwick* 7902 (P); Lafayette, *Davy* 1004 (C); Rocky Bluff, *Bruce* in 1897 (P); San Juan, *Elmer* 4635 (U. S.).

1e. *Orobanche uniflora* L. var. *Sedi* (Suksdorf), n. comb.

Aphyllon Sedi Suksdorf, Deutsch. Bot. Monatsschr. **18**: 155. 1900. *Thalesia Sedi* Rydberg, Bull. Torrey Club **40**: 485. 1913. *Orobanche Sedi* Fernald, *Rhodora* **28**: 236. 1926. *Orobanche uniflora* f. *Sedi* G. Beck, Pflanzenreich **4**²⁶¹: 48. 1930. *Aphyllon inundatum* Suksdorf, Allg. Bot. Zeitsch. **12**: 27. 1906. *Orobanche uniflora* f. *inundata* G. Beck, Pflanzenreich **4**²⁶¹: 49. 1930.

Pedicels 2–7 cm. long; corolla usually straw-colored, slightly curved, rarely spreading, tube 3–5 mm. wide at the throat, lobes truncate or oblong.

Type locality, Bingen, Klickitat Co., Washington. Ranging from British Columbia south through Washington, Oregon, California, Idaho, Utah, Montana, Wyoming and Colorado. Material seen—BRITISH COLUMBIA: Mt. Finlayson, *Pineo* in 1896 (C); Sproat, *Macoun* in 1890 (G); Victoria, *Fletcher* in 1885 (G). WASHINGTON: Bingen, *Suksdorf* 2642 (U. S., Suksdorf); Rock Creek, *Sandberg & Leiberger* 99 (U. S.); Blue Mts.,

Anoplanthus fasciculatus Walpers, Rept. 3: 480. 1844-45; *Aphyllon fasciculatum* Gray, Syn. Fl. 2: 312. 1878. *Thalesia fasciculata* Britton, Mem. Torrey Club 5: 298. 1894.

Pedicels 4-6 (rarely 10) in number, 3-10 cm. long; corolla usually purple, 15-22 mm. long, constricted at base of tube, lobes semiorbicular.

Type locality, Fort Mandon, North Dakota. Ranges from British Columbia and California to Michigan, Illinois, New Mexico and Arizona. Representative material—CANADA: Rosedale District, Alberta, *Moodie 1012* (G, U. S.); Sproat Lake, Vancouver Island, *Rosendahl 1940* (M, G). WASHINGTON: Tacoma, *Rensselaer* in 1894 (G); Ione, Pend Oreille Co., *Kreager 415* (G, U. S.); Blue Mts., *Horner 402* (G, U. S.). OREGON: Prairie City, *Henderson 5415* (G, M); Juniper Lake, Mono Co., *Hoffman* in 1930 (P); Lake Merced, *Brandegge* in 1907 (C); Montezuma Valley, *Jaeger 1926* (P); Cucamonga Peak, *Johnston 1556* (C, G, P); San Antonio Mt., *Johnston 1758* (P); San Jacinto Mts., Tamarack Valley, *Hall 2599* (C); San Bernardino Mts., *Parish 488* (U. S.); Cajon Pass, *Parish 19290* (C); Mt. Santiago, *Abrams 1849* (M); Catalina, *Minthorn* in 1920 (C). IDAHO: Weiser, Washington Co., *Jones* in 1899 (P); Picabo, Blaine Co., *Macbride & Payson 2991* (G, M, U. S.). UTAH: Lake Point, *Jones 2053* (P, U. S.); Salt Lake City, *Engelmann* in 1880 (M); Bear River, Summit Co., *Payson 4853* (P, M); Panguitch Lake, *Jones 6010* (C, M, P, U. S.). NEVADA: Washoe Mt., *Sonne* in 1888 (C); Charleston Mts., *Jaeger* in 1926 (P). ARIZONA: Chiricahua, *Blumer* in 1907 (G, M, U. S.). MONTANA: Wild Horse Island of Flathead Lake, *Jones* in 1908 (P); Bozeman, *Shear 5263* (U. S.). WYOMING: Pole Creek, *Nelson 1360* (G, M, U. S.); Headwaters of Mo. and Yellowstone rivers, *Hayden* in 1860 (M). COLORADO: Boulder, *Patterson 295* (C, G, M, U. S.); Salida, *Baker et al. 811* (M, P); Naturita, *Payson 363* (G, M). NEW MEXICO: Carrizo Mts. *Matthews* in 1892 (U. S.); Eagle Creek, Lincoln Co., *Woolon* in 1897 (U. S.). NEBRASKA: Council Bluffs, *Hayden 239* (M); Rush Creek, Deuel Co., *Rydberg 288* (U. S.). MICHIGAN: Manitou Island, *Engelmann* in 1840 (M). ILLINOIS: Dixon, *Vasey* in 1881 (M). INDIANA: Northwest, *Drew* in 1901 (C); Pine, *Chase 130* (G).

The variety *typica* has an unusually wide range and naturally a great variability, but I can not find characters permitting me to break it up. As a matter of fact the two varieties, *lulea* and *franciscana*, are not clear cut, as may be seen from the following intermediate forms.

The following intergrades with var. *lulea* have a tendency to be yellow like var. *lulea*. WASHINGTON: Breakmore, *Macoun & Herriot 2555* (P), *Flett* in 1898 (U. S.), *Merriam* in 1897 (U. S.). WYOMING: Dry Hills, *Leckie 798* (G); Alpine, Lincoln Co., *Payson & Armstrong 3397* (G, M, P).

As intergrades with var. *franciscana* may be cited the following specimens from California: (1) Santiago Peak, Orange Co., *Abrams 1847* (P), *1849* (M); there is a tendency for these to be light and not constricted at the base of the corolla tube, as is characteristic of var. *franciscana*; (2) San Jacinto Mts., *Spencer 1561* (P), *Hall 2154* (U. S.); these are shaped like var. *typica*, but the color and pubescence tends to be more like var. *franciscana*; (3) Laurel Hill Cemetery, San Francisco, *Eastwood 239* (G, U. S.); these are small and dark like var. *typica*, but otherwise they resemble var. *franciscana*, that is, they are not constricted at the base of the corolla tube and the lobes are not rounded.

2b. *Orobanche fasciculata* Nutt. var. *lutea* (Parry), n. comb.

Phelipaea lutea Parry, Am. Nat. 8: 214. 1874; *Aphyllon fasciculatum* var. *luteum* A. Gray, Syn. Fl. 2: 312. 1878; *Thalesia lutea* Rydberg, Bull. Torrey Club 36: 693. 1909; *O. fasciculata* f. *lutea* G. Beck, Pflanzenreich 4²⁶¹: 51. 1930.

Pedicels four to ten in number, 1–7 cm. long; corolla yellow and often tinged with lavender, slightly constricted at base, lobes usually acute; calyx lobes equal to or shorter than tube.

Type locality, Owl Creek, Wyoming. Ranging from Canada through eastern Washington and Oregon, to North Dakota, Nebraska, and Chihuahua. Representative material—ALBERTA: Banff, *McCalla* 2199 (U. S.); Rosedale, *Moodie* 58 (U. S.). WASHINGTON: Near Wilson Creek, Douglass Co., *Sandberg & Leiberg* 298 (M, C, G, U. S.); Chelan, *Jones* in 1911 (P); Columbia River, Klickitat Co., *Suksdorf* 2098 (C, G, M, U. S.), 2102 (C, G, M, U. S.); hills S.W. of Wallula, *Colton* 1051 (G, U. S.). OREGON: Grants Pass, *Prescott* in 1912 (M). IDAHO: Challis Creek, Custer Co., *Macbride & Payson* 3321 (G, M, U. S.); Squaw Butte, Canyon Co., *Macbride & Nelson* 146 (G, M); Big Potlatch River, Nez Perces Co., *Sandberg et al.* 308 (G, P, U. S.). MONTANA: Suksdorf Gulch, Park Co., *Suksdorf* 199 (P); Big Timber, Sweet Grass Co., *Eggleston* 7946 (U. S.); Gardiner, *Mearns* 1260 (U. S.). WYOMING: Mammoth Hot Springs, *Mearns* 1357 (U. S.); Owl Creek, *Parry* 202, type collection, (G, M); Platte River, Martono Co., *Gooding* 129 (M). COLORADO: Wet Mt. Valley, *Brandegee* in 797 (M); Fort Collins, *Baker* 5348 (P); South Table Mt., Golden, *Knowlton* 73 (U. S.). NORTH DAKOTA: Leeds, Benson Co., *Lunell* in 1916 (U. S.). SOUTH DAKOTA: Bald Hills, *Murdock* 5200 (G). NEBRASKA: Neligh, *Bacon* in 1896 (G); Pine Ridge, *Williams* 315 (U. S.). ARIZONA: Grand Canyon, *MacDougal* 159 (U. S.); Mormon Lake, *MacDougal* 78 (G). NEW MEXICO: Bear Mts., *Rusby* 331 (M); Valley of Rio Grande, C. C. *Parry et al.* 713 (U. S.). CHIHUAHUA: Sierra Madre, *Townsend & Barber* in 1899 (U. S.). SONORA: Puerta de St. Diego, *Hartman* 579 (G).

As here understood, var. *lutea* is more inclusive than is generally treated. Originally said to be parasitic on grasses, it has been so considered, but specimens cited above were on *Eriogonum*, *Artemisia*, and other hosts.

I have mentioned under var. *typica* some intergrades with var. *lutea*; the following are more like var. *lutea*, but suggest var. *typica* in being dark and in the corolla lobes tending to be rounded: OREGON: Lost Prairie, *Cusick* 2407 (G). COLORADO: Buena Vista, Chaffee Co., *Sheldon* 557 (U. S.); Arboles, *Baker* 610 (M). MONTANA: Spanish Basin, Madison Range, *Flodman* 797 (M, U. S.). SOUTH DAKOTA: Custer, *Rydberg* 936 (U. S.). ARIZONA: Grand Canyon, *Macbride & Payson* 966 (G). NEW MEXICO: Baranca, Taos Co., *Heller* 3585 (M, U. S.).

Not only do the following intergrades with var. *typica* tend to be dark, but the corolla is constricted at the base of the tube; COLORADO: Colorado Springs, *Knowlton* 59 (U. S.). CHIHUAHUA: Chuchuchupa, *Hartman* 703 (G, U. S.).

In the collection from Jackson Hole, Lincoln Co., Wyoming, *Payson* 2193 (G, M, P), the plants from the Missouri and Pomona herbaria are light like var. *lutea*, but the one from the Gray herbarium is dark like var. *typica*. Since the corolla lobes are acute, I have placed them here with var. *lutea* rather than with var. *typica* as I did the other specimens from Lincoln Co.

2c. *Orobanche fasciculata* Nutt. var. *franciscana*, n. var.

Pedicels four to twelve, 4–10 cm. long; corolla straw-colored or tinged with purple, not constricted at base of tube, lobes rounded, truncate or pointed; calyx lobes usually longer than tube. (Pedicelli quatuor ad duodecim, 4–10 cm. longi; corolla straminea vel subpurpurea, non infra constricta, lobis suborbicularibus; lobis calycis tuba longioribus.)

Type, Mt. Tamalpais, Calif., *Rydberg 6230*, June 15, 1905, Pomona College Herbarium No. 146628. Ranging west of the Sierra Nevada from southern Oregon to San Diego Co., California. Material seen—CALIFORNIA: Yreka, Siskiyou Co., *Greene* in 1876 (M); Hupa, *Manning 97* (C); near Middle Creek Station, Shasta Co., *Heller 7954* (G, M, U. S.); Fort Bidwell, Modoc Co., *Manning 383* (U. S.); Big Valley, Modoc Co., *Baker & Nutting* in 1894 (C); Humboldt Co., *Chestnut & Drew* in 1888 (C); Little Chico, *Austin 1912* (U. S.); Benicia, *Blasdale* in 1892 (C); Kirker's Pass, Contra Costa Co., *Brewer 1064* (U. S.); Paradise, Butte Co., *Bruce* in 1897 (P); Mt. Osa, *Brewer 1245* (C, G, U. S.); Mt. Hood, *Heller* in 1902 (G); Sonoma, *Bioletti* in 1892 (C); Mt. Eddie, *Austin 251* (C); Mt. Tamalpais, *Jepson* in 1892 (C), *Heller 8398* (U. S.), *Bioletti* in 1892 (C), *Michener & Bioletti* in 1892 (G, U. S.); hill north of Diablo, *Brewer 1124* (C, U. S.); Mt. Diablo, *Bioletti* in 1894 (C); Rawhide Hill, Tuolumne Co., *Williamson 63* (P, U. S.); Yosemite Valley, *Fritchey 29* (M); Copper Creek, Fresno Co., *Clemens* in 1910 (P); Stanford University, *Rutter 172* (U. S.); Owl Creek, *Parry 203* (G); Vaca Mts. *Jepson* in 1892 (U. S.); Kenworthy, San Jacinto Mts., *Munz & Johnston 5481* (P); Laguna Camp, San Diego Co., *Munz 8356* (P); Santa Catalina Isl., *Pendleton 1353* (P); Box Springs, near Riverside, *Corwin & Johnston 2896* (P); Julian, *Brandegee* in 1894 (C). OREGON: Near Ashland, Jackson Co., *Applegate 431* (G, U. S.).

This variety has intergradation with var. *lutea* and var. *typica*. In the collection from California: Yosemite Valley, "On State Survey" 27867 (C), the plant is yellow tinged with lavender as in var. *lutea*, and the corolla lobes do not spread as in var. *franciscana*. The specimen from California: Palm Springs, *Eastwood 3011* (G, U. S.) has glabrous anthers and is light yellow as in var. *lutea*. In the following collection, the corolla tends to be dark purple and strongly constricted at the throat as in var. *typica*; Bear Valley, San Bernardino Co., California, *Parish 3116* (U. S.). An intergrade with var. *typica* from Oregon: Crater Lake, *Coville 1481* (U. S.) is dark and the anthers are glabrous.

POMONA COLLEGE,
CLAREMONT, CALIFORNIA

Figs. 1–15. Fig. 1. Corolla limb of *O. uniflora* var. *typica*. Massachusetts: New Bedford, *Hervey* in 1890 (M). Fig. 2. Calyx of figure 1. Fig. 3. Corolla limb of *O. uniflora* var. *terrae-novae*. Newfoundland: Bard Harbor, *Wiegand et al. 29049* (G). Fig. 4. Corolla limb of *O. uniflora* var. *purpurea*. Washington: Bingen, *Suksdorf 2323* (M). Fig. 5. Calyx of figure 4. Fig. 6. Corolla limb of *O. uniflora* var. *minuta*. Washington: Pullman, *Elmer 43* (P). Fig. 7. Calyx of figure 6. Fig. 8. Corolla limb of *O. uniflora* var. *Sedi*. Washington: near Bingen, *Suksdorf 2642* (Suksdorf). Fig. 9. Calyx of figure 8. Fig. 10. Corolla limb of *O. fasciculata* var. *typica*. Utah: Panguitch Lake, *Jones 6010* (P). Fig. 11. Calyx of figure 10. Fig. 12. Corolla limb of *O. fasciculata* var. *lutea*. South Dakota: Black Hills National Forest, *Murdock 5200* (G). Fig. 13. Calyx of figure 12. Fig. 14. Corolla limb of *O. fasciculata* var. *franciscana*. California: Rawhide Hill, Tuolumne Co., *Williamson 63* (P). Fig. 15. Calyx of figure 14.



Figs. 1-15.

INDEX TO AMERICAN BOTANICAL LITERATURE 1930-1933

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A blue-green alga of carbonated mineral water

MARSHALL A. HOWE

(WITH PLATES 24 and 25)

Mr. Macey F. Deming of Tappan, New York, has directed the writer's attention to certain algae found on stones that have been piled up around the vent of a spring with geyser-like action at Saratoga Springs, New York, and apparently assisting in the deposition of crusts of calcium carbonate on such stones. Among these algae are species of *Microspora* and *Stichococcus* of the Chlorophyceae and a minute-celled member of the Myxophyceae (Cyanophyceae), the group more popularly known as the Blue-green Algae. The last-named is responsible for a striking blue-green or blue-purple coloration of the stones that attracts the attention of visitors. The spouting spring in question, according to information furnished by Mr. Herbert Ant, Senior Sanitary Chemist of the Saratoga Springs Commission, was formerly known as Pump Well No. 4, but was later renamed Polaris. The chemical composition of the water, he states, shows considerable variation from time to time. The water always contains large quantities of various soluble mineral salts, notably sodium chlorid, sodium bicarbonate, calcium bicarbonate, and magnesium bicarbonate. A rather recent analysis, made by Mr. Ant, is as follows:

Hypothetical combinations

Ammonium chlorid.	6.18*
Lithium chlorid.	2.15
Potassium chlorid.	154.02
Sodium chlorid.	1,135.01
Potassium bromid.	Trace
Potassium iodid.	Trace
Sodium sulphate.	Trace
Sodium metaborate.	Trace
Sodium nitrate.	Trace
Sodium nitrite.	Trace
Sodium bicarbonate.	741.14
Calcium bicarbonate.	1,407.31
Barium bicarbonate.	9.06
Strontium bicarbonate.	Trace
Ferrous bicarbonate.	10.51
Magnesium bicarbonate.	461.93
Alumina.	1.53
Silica.	10.80
Total solids	3,939.64

* Milligrams per liter.

[THE BULLETIN FOR JUNE (60; 379-464) WAS ISSUED JUNE 1, 1933.]

Phormidium Demingii sp. nov.¹

Forming thin (about 0.5 mm. thick) irregular cartilaginous, crustaceous, finally confluent, pulverulent-calcareous patches, externally aeruginous-olivaceous to blue-purple, internally prasinous, becoming minutely lacunose in older basal parts; filaments short (mostly 16–35 μ long when well developed), erect-ascending, parallel or somewhat flexuous and intertangled, very closely compacted, giving surface, under the microscope, a very minutely cellular Oncobyrsoid appearance; trichomes 0.8–1.4 μ in diameter; sheaths very soft and mucilaginous, wholly diffuent and invisible; cells (protoplasts) subquadrate, 0.7–1.6 μ long, 1–1 1/2 times as long as broad, very distinctly segregated, separated by 1/4–1/2 their own length, apical cell rounded-obtuse; trichomes often dissolving into hormogonia of one or two cells which grow out in various directions, giving irregular or confused effects.

Forming a calcareous coating on stones that are kept continuously wet by the spray of the Polaris Spring, Saratoga Springs, New York, Macey F. Deming, October, 1932.

In its minute subquadrate cells and in its habitat, *Phormidium Demingii* may suggest *P. foveolarum* (Mont.) Gom. (type from roadside between Magny en Vezin and Mantes, France), but it differs amply in color, in the much shorter, less rigid, less moniliform, erect-ascending filaments, in the relatively longer and more widely spaced protoplasts, etc. The pulverulent calcification is perhaps not to be considered a diagnostic character, for considerable areas, microscopically speaking, show no lime. See also the observations of Frémy on *Rivularia dura* (Ann. Protistol. 3 (2/3): 69–79. 1931).

In its mostly erect-ascending filaments, *Phormidium Demingii* is slightly suggestive of *Oncobyrsa Cesatiana*, but, in spite of the frequent occurrence of solitary or geminate cells, the structure is essentially filamentous and not Chroococcaceous. In surface view, under the compound microscope, the structure may seem to be minutely cellular rather than filamentous, but that is because most of the filaments present their apices to the observer.

¹ Stratum externe aerugineo-olivaceum aut, in siccitate, caeruleo-purpureum, interne prasinum, tenue (ca. 0.5 mm. crassum), irregulare, cartilagineum, crustaceum, pulverulenti-calcareum. Fila brevita (plerumque 16–35 μ longa, quum bene evoluta), erecti-ascendentia, subparallela aut plus minusve flexuosa et intricata, compacta, superficie strati minute cellulosa sub microscopia visa. Vaginae in mucum gelatinosum amorphum hyalinum diffuentes. Trichomata prasina, 0.8–1.4 μ crassa. Cellulae (protoplasta) subquadratae, 0.7–1.6 μ longae, 1–1 1/2-ies longiores quam latae, distincte segregatae, a 1/4–1/2 suae longitududinis separatae, cellula apicali rotundati-obtusa. Hormogonia uni-aut bi-cellularia frequentes et, quoqueverse crescentia, facies confusas saepe fingentes. Planta stratum calcareum in lapidibus irroratis ad "Polaris Spring," in urbe Saratoga Springs, Novae-Eboracae, efficit. Legit Macey F. Deming, Oct. 1932.

One finds occasional larger ovoid cells, about 3μ in diameter, single or aggregated, with suggestions of division into smaller cells, but they occur chiefly in older, interior parts of the colonies and it is probable that they are intrusions of another organism—probably a member of the Chroococaceae. There are rarely, however, conglomerations of small cells that evidently belong to the species here described, but they may be fortuitous aggregations of cells floating in the mounting fluid rather than gonidia in a gonidangium. The minuteness of the cells and the absence of any visible cell walls make accurate observation difficult and erroneous inference easy. If sporangia or gonidia are really present, the organism would seem to find its proper affinity in or near *Radaisia* of the Chamaesiphonaceae. However, there is no attachment of the filaments in the stages studied.

Associated with our plant are occasional more or less isolated filaments of the more conventional *Phormidium* type—longer, slightly broader, much more rigid, with obscure dissepiments and longer protoplasts—perhaps closely allied to *Phormidium tenue* (Menegh.) Gom.

The water of the Polaris Spring is, at the time of its discharge, supersaturated with carbon-dioxide gas.² Although intermittent, the discharges of the Polaris Spring are so frequent that the algae on the sprayed stones do not have an opportunity to dry out. As the water falls on the stones, the gas is released in the form of small bubbles (plate 24, fig. 2), so that the algae are continuously bathed in a fizzing highly mineralized water. It is probable that, whether carbonated or not, the waters in which the primordial algae lived were richer in mineral salts than those in which most of our so-called freshwater algae of the present day are found, so that the alga described above as new is of interest in the biologic as well as the systematic field.

THE NEW YORK BOTANICAL GARDEN

² The report of Dr. David H. Newland states that in some of these Saratoga springs "the waters contain as much as five or six volumes of carbon dioxide." N. Y. State Mus. Bull. Nos. 223, 224: 159. 1921.

Explanation of plates 24 and 25

Plate 24

Fig. 1. Type locality of *Phormidium Demingii*, the crusts of which may be seen, especially on the larger lower stone at the right. The vent of the Polaris Spring, Saratoga Springs, N. Y. Photograph by M. F. Deming, October, 1932.

Fig. 2. Water from the Polaris Spring, showing release of carbon dioxide. Photograph by M. F. Deming.

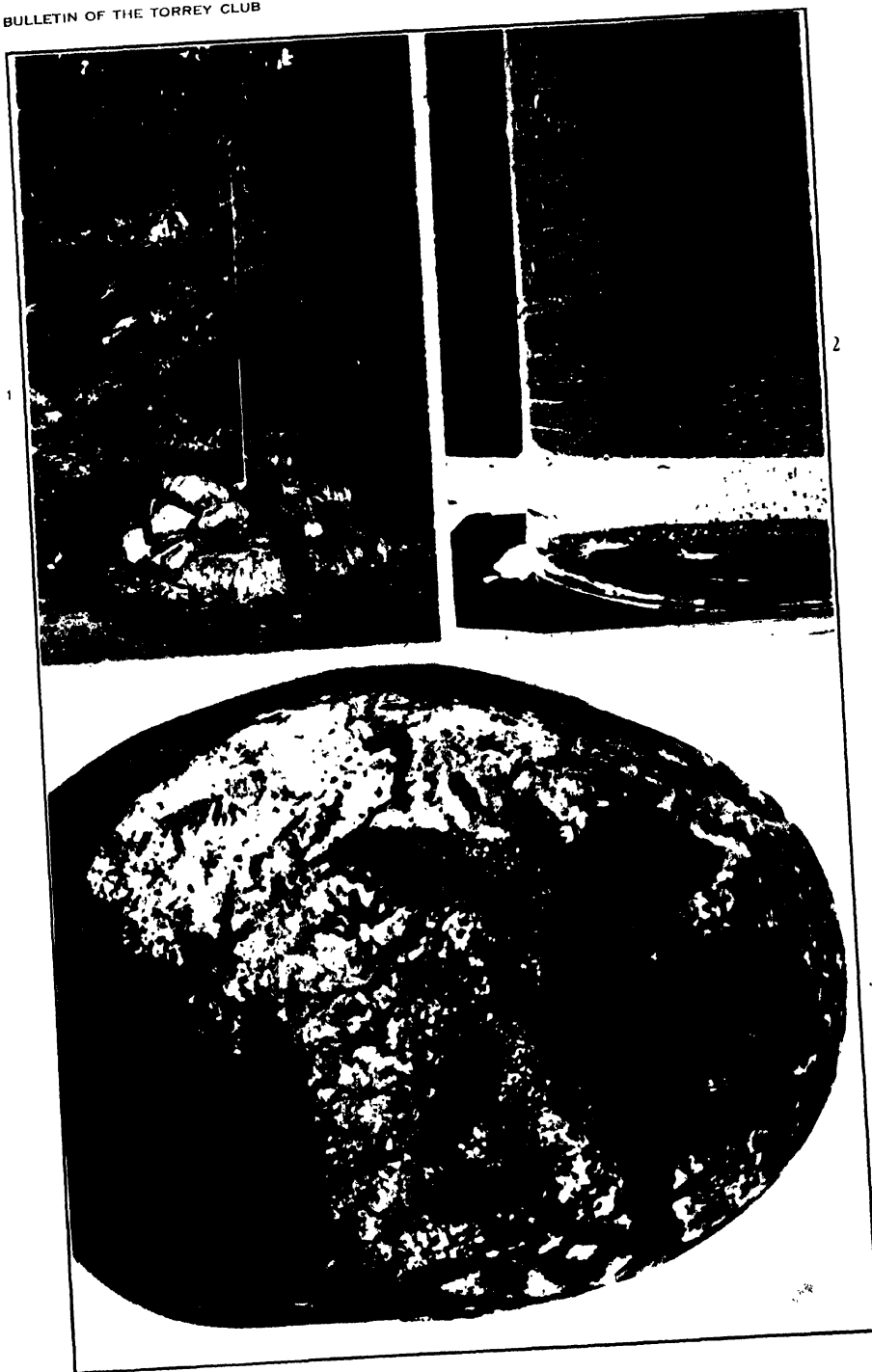
Fig. 3. A stone from the Polaris Spring, showing the calcareous crusts of *Phormidium Demingii*, here appearing white. Natural size.

Plate 25. *Phormidium Demingii*

Fig. 4. Photomicrograph of vertical microtome section through a crust, $\times 580$.

Fig. 5. A teased-out preparation of decalcified material, $\times 610$.

Fig. 6. A similar preparation, $\times 690$.



HOWE A BLUE-GREEN ALGA



HOWE A BLUE GREEN ALGA

On potato catalase

H. H. BUNZELL AND MARJORIE B. KENYON

(WITH TWO FIGURES)

INTRODUCTION

Since the discovery of hydrogen peroxide decomposition by animal and plant tissues (Schönbein, 1863) and the naming of the specific enzyme responsible for this reaction by Loew (1901), much work has been done so that we may learn what rôle catalase plays in the metabolism of plants and animals. The oldest view is that expressed by Loew and later Wieland (1928) that it protects the cells against the hydrogen peroxide formed in the course of photosynthesis and metabolism. For a detailed discussion of the plausibility of this function we refer to the paper of Dakin (1921) and Knott (1927). To date all evidence tending to show the formation of hydrogen peroxide in plant cells is not conclusive and the alleged protective action of catalase is therefore purely speculative.

More suggestive of a definite function of catalase is the work of Appleman (1915) and that of Pope (1932). Appleman studied the catalase activity and oxidase activities of potato juice and simultaneously the intensity of respiration of the tubers from which the juice was obtained. His principal conclusions were firstly, that there is no correlation between oxidase activity and the rate of respiration of the tubers and secondly, that there is a very striking correlation between catalase activity and the rate of respiration of the tubers.

The senior author (1914) studied the oxidases of growing potato plants in Houlton, Maine. The oxidase activities of tubers and foliage toward eighteen different oxidase reagents were determined at different stages of development. In the case of the tubers there appears to be no definite trend of the oxidase activity during growth. The oxidase activity of the foliage of normally developing potato plants is greatest in the early stages of development; it falls off with growth of the plants and rises again when the plants' growth about reaches a standstill. It was also found that the juice of the tubers is in all cases several times as active as the juice of the foliage.

The experiments were carried out by means of the manometric method (1912) for determining oxidases. Quite recently we developed a manometric method for catalase determination (1930a, 1930b, 1932). To learn what relationship, if any, exists between catalase content and oxidase content in growing potatoes, it seemed desirable to carry out experiments similar to those performed in Maine, determining the catalase activity at

different stages of development. The plantings were made by the junior author in Hastings, Michigan.

METHODS

Petoskey Russet potatoes were planted. Great care was taken to have uniform conditions in the soil and in the manner of planting. The plants were pulled at 6:00 A.M., washed with tap water and dried by first gently patting with a linen towel and then hanging in a strong breeze for five minutes. Each plant was then weighed. The leaves were separated from the stems and ground through the "butter knife" of a food grinder. Catalase determinations, Bunzell (1930) method, were run on weighed samples of this pulp so obtained. Catalase determinations were also run on the juice obtained by straining the pulp through fine muslin. The stems and tubers were treated in the same manner as the leaves. Catalase determinations were run on the tubers before planting and also on the pieces of seed tuber adhering to the plant.

RESULTS

Appleman (1910, 1911) found the catalase activity of potato pulp rather unstable. We therefore first performed some experiments showing whether within the duration of the experiment there was marked loss in catalase activity. The results are shown in table 1.

TABLE 1

POTATO PULP			POTATO JUICE		
TIME	MM. OF MERCURY	CATALASE UNITS	TIME	MM. OF MERCURY	CATALASE UNITS
Immediately			Immediately		
After Grinding	20.0	1371	After Grinding	18.0	1234
30 min.	20.0	1371	30 min.	20.0	1371
1 hour	20.0	1371	1 hour	20.0	1371
2 hours	18.0	1234	2 hours	18.0	1234
4 hours	16.0	1097	4 hours	13.0	901

It is evident that in both the potato pulp and the potato juice the catalase activity remains constant, within experimental errors, for at least an hour and soon after that, shows gradual diminution. Inasmuch as our determinations were completed within less than one hour after preparation of sample, no error is introduced through standing.

The catalase content of the various parts of the potato plant at different stages of development is shown in tables 2 and 3 and figures 1 and 2. Table 2 and figure 1 give results obtained on pulp while table 3 and figure 2 on the expressed juice.

TABLE 2
Catalase activities of different parts of potato plant at different stages of development (pulp)

AGE OF PLANT (DAYS)	WEIGHT OF PLANT	NUMBER OF TUBERS	TOTAL WEIGHT OF TUBERS	SEED POTATOES	CATALASE ACTIVITY EXPRESSED IN CATALASE UNITS ^a			
					SHOOTS	LEAVES	STEMS	TUBERS
15	5.5			14303.7	14563.0			
22	14.4			14942.5		46322.0	17980.0	
29	41.9			15211.0		44615.0	15050.0	
35	66.5			13685.0		47538.0	14468.0	
43	229.1					60916.0	16613.0	
51	289.6	9	29.7			48230.0	12400.0	19290.0
58	513.9	11	195.6			80986.0	14410.0	22545.0
65	481.0	11	286.2			81300.0	13780.0	20670.0
71	453.6	11	445.8			65468.0	14591.0	19094.0
73	727.9	10	855.4			74680.0	14520.0	23508.0
103								13710.0

^a Based on oxygen pressure produced by one gram of material in five minutes.

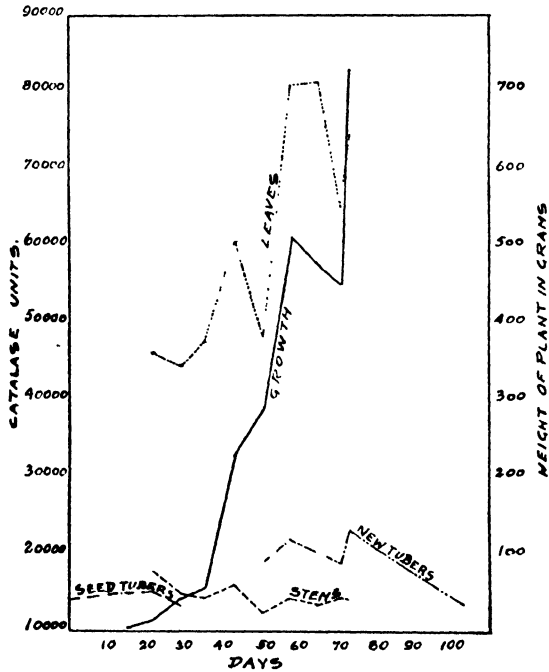


FIGURE 1.
CATALASE ACTIVITIES OF PULP AND JUICE MIXTURE.

DISCUSSION

There appears to be no parallelism between the oxidase activity and the catalase activity when the different parts of the potato plant are sepa-

TABLE 3
Catalase activities of different parts of potato plant at different stages of development (expressed juice)

AGE OF PLANT (DAYS)	WEIGHT OF PLANT	NUMBER OF TUBERS	TOTAL WEIGHT OF TUBERS	SEED POTATOES	CATALASE ACTIVITY EXPRESSED IN CATALASE UNITS ^a			
					SHOOTS	LEAVES	STEMS	TUBERS
15	5.5			16174.5				
22	14.4			18372.0				
29	41.9			11754.0		41848.4	15190.0	
35	66.5			13685.0		46529.0	13685.0	
43	229.1					45470.0	12400.0	
51	289.6	9	29.7			47071.0	17308.0	
58	513.9	11	195.6			44037.0	13090.0	14465.0
65	481.0	11	286.2			68616.0	13024.0	23338.0
71	453.0	11	445.8			77160.0	12400.0	20670.0
73	727.0	10	855.4			64104.0	12960.0	19094.0
103						77428.0	13826.0	24988.0
								13710.0

^a Based on oxygen pressure produced by one cubic centimeter of juice in five minutes.

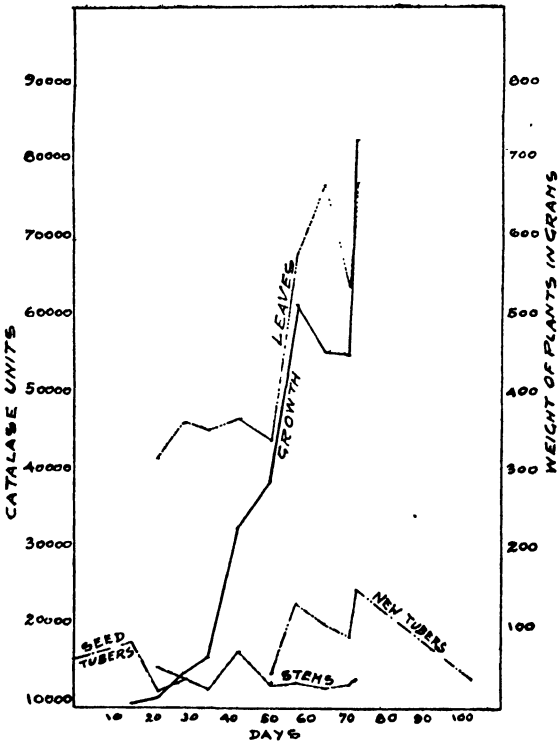


FIGURE 2.
CATALASE ACTIVITIES OF STRAINED JUICE.

rately investigated. The two enzymotic activities certainly do not run parallel, in fact there is some indication that they are in some kind of reciprocal relationship. This latter conclusion is supported by the following evidence.

A. With all oxidase reagents which showed pronounced oxidizability in the presence of potato oxidase, the activity was much greater in the tubers than in the foliage. The catalase activity on the other hand, was constantly two to four times greater in the foliage than in the tubers of the same plants.

B. The oxidase activity of the foliage of healthy potato plants is greatest in the early stages of development; it falls off with the growth of the plants and rises when the plants' growth about reaches a standstill. The catalase activity of the foliage of normally developing potato plants is lowest in the early stages of development, increases with the growth of the plant and diminishes again when the plant reaches full growth.

C. As the average weight of tubers increases from 8.8 grams to 60.0 grams, no constant trend in oxidase activities could be found. The oxidase activity toward some reagents (p-cresol) increases pronouncedly, while it diminishes when other reagents (phloroglucin, resorcin) are used. In case of certain reagents (guaiacol, pyrogallol) there is irregular fluctuation. In the case of catalase activity the situation is different. While very small tubers (3 g.) and fully matured tubers show lower catalase activity, throughout the principal period of growth the catalase activity of the juice of the tubers stays fairly uniform.

This opposite behavior of oxidase activity on the one hand, and catalase activity on the other, is also borne out by the literature. Appleman (1915) finds a slightly lesser oxidase activity in the seed end of potato tubers when compared with the stem end. The catalase activity is much greater in the seed end than in the stem end. In this respect catalase activity runs parallel with respiratory activity which is greater in the seed end than in the stem end. Appleman compared two varieties of potato (McCormick and Carmin no. 1). He found McCormick to have about four times the oxidase activity of Carmin no. 1, while the catalase activity was about twenty-five percent greater in Carmin no. 1 than in McCormick. Ezell and Crist (1927) studied the effect of various plant nutrients on oxidase and catalase activities of lettuce, radish and spinach. In general the oxidase activities fluctuate only within narrow limits, while the catalase activity varies greatly. Reed (1916) in his work on fruit showed that in the process of ripening the catalase activity increased while the oxidase activity stayed constant.

In 1916 the senior author expressed the belief that only a certain por-

tion of a commonly occurring colloidal constituent, such as protein, is responsible for oxidase activity. This active fraction may be in a peculiar colloidal state and the fractional amount of the total may vary from plant to plant and also from one part of a plant to another. It is conceivable that a different degree or type of colloidalness would be responsible for the catalase activity. The two types of colloidalness would be so interrelated that each operates to the exclusion of the other. In this way a greater catalase activity would be found concurrently with lower oxidase activity and vice versa.

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New genera and species of Uredinales¹

J. C. ARTHUR

Cumminsiella Arth. nov. gen.

Pycnia subepidermica, paraphysata. *Aecia* subepidermica, cupulata, peridio instructa; *aeciosporae* globosae; *episporia* hyalino, verruculoso. *Uredia* subepidermica, interdum paraphysata; *urediosporae* solitarie natae, obovoidae vel subfusiformae; *episporio* brunneo, verrucoso, poris germinationis equatorialibus vel in series duas dispositis praeditis. *Telia* subepidermica; *teliosporae* solitarie natae, 1-septatae; *episporio* brunneo, verrucoso, quaque cellula poris germinationis 2 lateralibus dispositis praeditis.

This genus is established to segregate from the genus *Uropyxis* those species having subepidermal pycnia and cupulate, aecidioid aecia. So far as known the species of this genus occur only on the genus *Mahonia* of the Berberidaceae and include the three following North American species, the first representing the type: ***Cumminsiella sanguinea*** (Peck) Arth. nov. comb. (*Uromyces sanguinea* Peck, Bot. Gaz. 4: 128. 1879, *Puccinia mirabilissima* Peck, Bot. Gaz. 6: 226. 1881, *Uropyxis mirabilissima* Magn., Ber. Deutsch. Bot. Gessel. 10: 193. 1892, *Uropyxis sanguinea* Arth., N. Am. Flora 7: 155. 1907); ***Cumminsiella Wootoniana*** Arth. nov. comb. (*Uropyxis Wootoniana* Arth., Bull. Torrey Club. 42: 585. 1915); ***Cumminsiella texana*** (Holw. & Long) Arth. nov. comb. (*Puccinia texana* Holw. & Long, Bull. Torrey Club 29: 113. 1902, *Uropyxis texana* Arth., N. Am. Flora 7: 155. 1907, *Aecidium Bullerianum* Rosen & Arth.; Rosen & Kirby, Phytopath. 9: 572. 1919.)

Hammarlund, with *C. sanguinea*, now widely distributed in Europe, was the first to establish by cultures the presence of aecidioid aecia in this genus (Bot. Notiser 1930: 380. 1930; same 1932: 406. 1932). The assignment of *Aecidium Bullerianum* to *C. texana* is not yet substantiated by cultures. No aecia are known for *C. Wootoniana*.

In general appearance this genus resembles *Puccinia* and produces aecia of the same kind. The shape of the urediospores and the arrangement of the pores as well as the laminate wall of the teliospores with 2 lateral germ pores in each cell seems to indicate relationship with the *Uropyxideae-Ravenelieae* group of rusts.

The generic name is given in honor of Mr. George B. Cummins who has done commendable work in the taxonomy of the Uredinales.

¹ Contribution from the Botany Department, Purdue University Agricultural Experiment Station, Lafayette, Ind.

Uraecium Arth. nov. form. gen.

Pycnia subcuticularia vel subepidermalia. Aecia sine peridio, interdum paraphysata; aeciosporae pedicellatae.

None of the previously recognized form-genera adequately cares for isolated species having pycnia and uredinoid aecia (so-called primary uredia). The following two species are included in the genus, the first being taken as the type: **Uraecium Holwayi** Arth. nov. comb. (*Uredo Holwayi* Arth., Bull. Torrey Club 33: 518. 1906; **Uraecium lucumae** (Arth. & Johnston) Arth. nov. comb. (*Uredo lucumae* Arth. & Johnston, Mem. Torrey Club 17: 169. 1918).

Uredo tacita Arth. nov. spec.

Uredia hypophylla, sparsa, pulverulenta, flavo-brunnea; urediosporae globosae vel ellipsoidae, $19-23 \times 23-28\mu$, episporio pallide brunneo, 2μ cr., echinulatae, poris germ. 5-8, sparsa.

On *Digitaria Gardesii* (Hack.) Parodi, Mandaque, São Paulo, Brazil, May 25, 1922, E. W. D. & Mary M. Holway 1887. The host was determined by Dr. A. S. Hitchcock.

Aecidium Hesleri Arth. nov. spec.

Pycnia epiphylla. Aecia hypophylla, maculis orbicularis usque 5 mm. diam. insidentia, gregaria, cupulata; cellulis peridii firme conjunctis, rhomboideis, $15-18 \times 23-30\mu$; pariete exteriore $4-6\mu$ cr., striato, interiore 3μ cr. verrucoso, aeciosporae globosae, $11-13 \times 13-16\mu$, episporio $0.5-1\mu$ cr., hyalino, minute verrucoloso.

On *Lithospermum tuberosum* Rugel, near Jasper, Marion Co., along a small stream (Battle Creek), Tenn., May 2, 1931, H. M. Jennison & A. J. Sharp. Communicated by Dr. L. R. Hesler under herbarium no. 350 of the University of Tennessee.

This *Aecidium* differs from the boraginaceous aecia of *Puccinia rubigovera* by its more delicate aecia and especially by the small size of the aeciospores.

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A new Piper from British Guiana

WILLIAM TRELEASE

Piper Grahami Trel., sp. nov. Frutex 1.5 m. altus, *P. dilatato* similis; axibus, petiolis, et nervis subtus plus minusve persistenter crispo-pubescentibus; internodiis superioribus gracilibus, satis celeriter elongantibus; foliis subrhombice elliptico-obovatis acuminatis, 7-8 cm. latis, 15-18 cm. longis, in sicco tenues et firmi, basi angustata rotundata in latere uno breviori, nervis pinnatis 5×2, infra medium orientibus, a nervulis transversalibus connexis; petiolis 8-10 mm. longis, 2 mm. crassis, prope basin vaginantibus; spicis obtusis, adhuc 55 mm. longis, 2 mm. crassis, pedunculis vix 5 mm. longis; bracteis rotundato-subpeltatis.

A shrub, 1.5 m. tall, in aspect of foliage resembling *P. dilatatum*; axes petioles and nerves beneath more or less persistently crisp-pubescent; upper internodes slender, rather quickly elongating; leaves subrhombically elliptic-obovate, acuminate, the narrowed base rounded, somewhat shorter on one side, 7-8 cm. broad ×15-18 cm. long, pinnately nerved from the lower half, the nerves 5×2, with connecting cross-veins, drying thin and firm; petiole 2 mm. thick ×8-10 mm. long, sheathing near the base; spikes as yet 2 mm. thick ×55 mm. long, blunt; peduncle scarcely 5 mm. long; bracts rounded-subpeltate.

Type: Kyk-over-al, junction of the Mazaruni and Cuyuni Rivers, British Guiana, July 9, 1924, *Graham 227*. Graham's field notes give "5 ft. high; aments white when young." Kyk-over-al is a small island in the Mazaruni River where it joins the Cuyuni. The island, which was once cleared by the Dutch who inhabited it and where the ruins of their fortress still stand, was covered with second-growth jungle when the plant was collected.

The species has been named for the collector, Dr. Edward H. Graham, Assistant Curator of Botany at the Carnegie Museum who has in press a local flora of the Kartabo region, British Guiana. The plant is similar to *P. dilatatum* Rich., from which it differs chiefly in the villousness of the nerves beneath and the glabrousness of the leaves above. The type specimen is in the Herbarium of the Carnegie Museum at Pittsburgh, Pennsylvania, with duplicates at the New York Botanical Garden at New York City and at the Herbarium of the University of Illinois, Urbana, Illinois.

Tertiary pollen—II

The oil shales of the Eocene Green River formation

R. P. WODEHOUSE

(WITH 56 TEXT FIGURES)

The Green River oil shales of Colorado and Utah are believed to have been deposited in shallow lakes. The conditions under which the deposition took place were such that the pollens which fell upon the surfaces of these waters and sank to the bottom, became permanently imbedded in a translucent gelatinous organic matrix, which later became oil shale, and in which they may be observed today just as they fell, though this took place probably about forty million years ago.

Thus the oil shales hold an ancient pollen record of the same kind as that which forms a part of all pollen surveys today. In pollen surveys microscope slides bearing some transparent adhesive substance, such as glycerine jelly, are exposed out of doors, and every day they are examined and the pollen grains which are caught by the adhesive are identified and counted. In this way the different kinds of pollen floating in the atmosphere of the locality are learned and a record is kept of their abundance from day to day. In the following pages are presented identifications of some of the pollen that floated in the atmosphere and was caught by the Green River lakes in Middle Eocene time.

There are literally thousands of pollen grains in the shales. Frequently they are packed so thickly that they overlap each other making observation difficult. They are far too numerous to permit a complete count of the different species. In the present work only those identifications are recorded which I feel are reasonably certain and close as to the family. These constitute only a relatively small proportion (possibly less than one-third) of the identifiable pollen. The remainder will have to await a considerable extension of our knowledge of pollen morphology. No attempt was made to count the grains of the species which were identified, this is a subject reserved for later study, but in describing each species some note is generally made of my impression of its relative abundance.

In many cases where pollen was identified as belonging to a genus which is already represented in the Green River flora, there is a temptation to refer the pollen to the previously recorded species of that genus. This, of course, cannot be done until the pollen is found in organic connection with the plant to which it belongs. As far as I know this has never been done for pollen from Tertiary deposits, though the reverse is true of much more ancient formations. In fact, most of the known Paleozoic pollen has been

described either from the anthers or pollen chambers of the Pteridosperms and Cordaitales to which they belong. When, therefore, fossil aments or flowers with anthers containing recognizable pollen are found, I would urge that the pollen be examined and carefully recorded, or be submitted to a pollen morphologist to be studied in detail, for only in this way can the pollen species ever be linked with certainty with the fossil plants to which they belong. When this knowledge is gained the value of the fossil record can be enormously extended.

The materials used in these studies consist of nine microscope slides, of which seven are microtome sections of oil shales and two are ground sections of chert concretions from the oil shales. These were very kindly loaned to me for study by Dr. W. H. Bradley of the U. S. Geological Survey. They have already been reported upon by him in his studies of the algae of the Green River formation (15), and more extensively, with a short discussion of their pollen content, in his report on the origin and microfossils of the oil shales (16). In fact, the present paper is an extension of the pollen work initiated there.

The material from which these slides were prepared came from the upper oil shale group of the Parachute Creek member of the Green River formation, most of it from a single group of beds known as "Mahogany Ledge" (see Bradley, 16, pl. 7).

Like all other paleobotanical identifications, those of pollen grains are always made with some uncertainty. The value of all such identifications is exactly proportionate to the degree of probability of their correctness. In the last analysis, the identification of pollen must always be based upon comparisons with living species, or with previously recorded fossil forms, as is the identification of leaves, stems, seeds, and various other parts of plants. The botanist of fossil pollen does not have available reference collections comparable in extent to the large herbaria which are at the disposal of other paleobotanists. Nor has he knowledge of the structures of pollen grains and their phylogenetic significance which is in any way comparable to that which is the common heritage of other paleobotanists with their material. It is to be hoped, therefore, that the value of such pollen-grain identifications as these will be made sufficiently apparent by workers in this field to warrant the building up of collections of permanently mounted pollen slides comparable in extent to the great herbaria of the world, and that capable workers will be attracted to study and to portray the pollen forms, as has been done with other plant structures. Until this gap is filled, the fossil-pollen botanist must build up and interpret his own reference collections to meet his needs as the work of identification pro-

gresses, and the degree of reliability of his identifications will depend largely upon the extent of his collections and his understanding of them.

In the present work I had at my disposal a nucleus collection of two or three thousand slides, prepared and studied by myself, including species of practically all the wind pollinated genera of North America, and many from various other countries. As the work of identification progressed, I added to my collection the pollen of living representatives of the Green River flora (Wodehouse, 46). This was later extended by the addition of pollen of the majority of the living representatives of the entire Eocene flora. My own estimate of the probability of the correctness of the identifications is generally included with the description of each species.

Fossil pollen has been reported from time to time for many years and from most of the geological formations where records of spermatophytes are found. For the most part such reports have been only casual mention of pollen found in connection with other paleobotanical studies. More recently, however, it has become generally known that pollen has been preserved in enormous quantities in post-glacial, and inter-glacial peats, and many such deposits have been intensively studied, particularly in Europe. It is found that the pollen in such peats can be identified with a fair degree of certainty, and from a study of the incidence and distribution of the different kinds in time and space there has been obtained much valuable information regarding the history of the vegetation and climatic conditions in various parts of the world since the Pleistocene glaciation. Though scores of investigators are now working on Recent deposits, only very few have devoted themselves to earlier deposits of similar kind. One of these is Robert Potonié (38, 39, 40, 41). He has described many different kinds of pollen from European Eocene and Miocene brown coals. Some of the pollen species he has found possible to refer to living genera, but the majority are described and illustrated without attempting their identification, for, it is pointed out, even these records, without a knowledge of the identity of the pollen, are valuable in characterizing the brown coals in such a way that they may be recognized by microscopic examination. Potonié says, however, that both wind-borne and insect-carried pollen are found in the coals; though the former might have been blown in from distances, the latter, such as the pollen of the Ericaceae which is found in considerable quantity, must have originated *in situ*. In some of the moors of localities similar to those where the coals were obtained, species of the Ericaceae are growing, and Ericaceous pollen is found in the top layers of the peat. Presumably, therefore, conditions were about the same when the Tertiary brown coals were laid down, as now.

A work similar to that of Potonié is being conducted by Kirchheimer (24, 25). He has described and illustrated many species of pollen from Eocene brown coals and has succeeded in arranging them according to a system modified from the classification of Fischer (23), and some of the fossil pollen he has identified as that of living genera. Apart from these studies I do not know of any other reports on the pollen of Tertiary deposits.

In the work of these and earlier investigators pollen species are always designated as *Pollenites* or *Pollinites* followed by the specific name proposed by the author and preceded by the generic name when this is known or suspected. The use of the word *Pollinites* has the value of pointing out the fact that the object so designated is a fossil pollen grain, but it is without other significance because, designating all pollen, it becomes universal and designates nothing, and its monotonous repetition takes up space to no purpose other than to tell that the fossil, which we already know to be a pollen grain, is a fossil pollen grain. Consequently I propose, and have here adopted, the following system of nomenclature. The word *Pollinites* is retained for its slight value in indicating the general nature of the object under consideration, but it is contracted to '*-pites*' and used as a suffix applied to the specific designation if the genus of the pollen species is known with the normal degree of accuracy, otherwise, to its generic designation. Thus a grain which is certainly that of *Pinus*, and which resembles most closely that of the living *Pinus Strobus*, is called *Pinus strobipites*. And the pollen of *Ephedra*, which is the first record of the genus in the Eocene in America, may be called *Ephedra eocenipites*. But, if the genus is not accurately or certainly known, the termination '*-pites*' is applied to the generic designation of the fossil grain instead of to its specific designation. Thus a grain which is known to belong to the Ericaceae, but the genus of which cannot be determined, is called *Ericipites longisulcatus*, for example, the specific name having reference to the length of its furrows. And a grain that matches the living species of *Smilax* but also matches almost equally well those of some other genera is called *Smilacipites molloides*, for example, its specific designation referring to its further resemblance to the grains of the living *Smilax mollis*. If at some later date any of those genera which bear the termination '*-pites*' should become more closely defined or proved to be accurately determined, the termination may then be transferred to the specific names. The advantages of this system are that complete freedom is allowed in the use of descriptive adjectives as specific names without the introduction of trinomials, some idea is conveyed of the closeness or reliability of the determination, and always is shown the fact that the determination is based on a fossil pollen grain.

Some of the species described here appear to be very similar to some of those described by Pontonié and Kirchheimer and indeed may be the same, but for none was I able to prove this entirely to my satisfaction, consequently I have described them all as new. The descriptions are always based upon as many grains as were found suitable for detailed examination, but only a single one is chosen as the type, selected either because I regarded it as most typical or because it seemed to show the characters to the best advantage.

The slides upon which the descriptions are based will be permanently lodged with the U. S. Geological Survey, and in order that other pollen specimens may be compared with those described here, the locations of the holotypes among the slides are indicated after each description by three numbers. The first number designates the slide, the second the ordinate and the third the abscissa reading of the stage micrometer. The stage used was made by Carl Zeiss, known as 'mechanical stage E,' and the divisions of the scale are in millimeters and tenths. If the same type of stage is used and properly centered all of the holotype readings may be readily picked up. In order to facilitate finding the holotypes when other kinds of stages are used, I have supplied a reference point on each of the slides indicated by a conspicuous cross (+). The readings of these are as follows: 3-15.2-54.2; 4-9.7-48.9; 5-20.8-53.9; 6-11.1-48.8; 8-9.5-50.6; 17-13.9-51.0; 36-24.0-73.1; 25/6-14.9-62.7; 25/8-19.5-55.2.

If these readings are compared with the readings for the same points using any other mechanical stage and the numerical differences added to or subtracted from the readings of the holotype, the latter may be found with any microscope which has a mechanical stage providing its micrometer scales are divided into millimeters.

CYCADACEAE

Cycadopites gen. nov.

Essentially as in living species of *Cycas*, but larger. Ellipsoidal, about twice as long as broad, 25-45 μ long; provided with a single longitudinal furrow, reaching almost from end to end and always gaping open at its ends, even when tightly closed in the middle. Exine thin but firm, of various texture but generally quite smooth.

In the oil shales are a great many grains of this description. These occur in various conditions of collapse which can be matched among the grains of species of *Cycas* and *Zamia*. That they belong to the Cycadaceae seems tolerably certain, but I have made no attempt to distinguish the different genera and species from each other for this is rarely possible even with living material.

Three grains are figured (figs. 1, 2, 3), but since they possess no differentiating characters, except possibly that of size, they are shown here principally as examples of the various forms of collapse that such grains undergo.

Dioonipites gen. nov.

Spherical or more or less invaginated on one side, $28.5\text{--}34.2\mu$ in diameter. Exine rather thick, minutely pitted and of uniform thickness throughout, presenting a radially striate appearance in optical section.

The position of this genus among the Cycadaceae is not certain. Five specimens were found. Three are quite spherical and without any suggestion of a germinal furrow, one has a slight indentation (fig. 4) while the fifth is flattened on one side with a well developed rim which suggests that in life it had a deep furrow (fig. 5). These can be matched in form perfectly with grains of *Dioon spinulosum*, and the latter range in size from $26\text{--}29.5\mu$ in diameter. The grains of *Dioon* are exceptional among those of the Cycads in two important respects; their whole surface, including the furrow floor, is finely pitted, and when moistened the evagination of the furrow may be so complete that the grain becomes almost perfectly spherical, showing little or no suggestion of its former furrow. In the pollen of *Dioon spinulosum* which I have examined, grains occur in the three conditions which are represented by the fossil specimens.

The grains of the Araucarineae also bear a marked resemblance to these in form so that there is a possibility that they may belong to that group, but those of the only two species available for comparison, one species of *Araucaria* and one of *Agathis*, are $41\text{--}91\mu$ in diameter, much too large to compare with those of the present species.

CONIFERAE

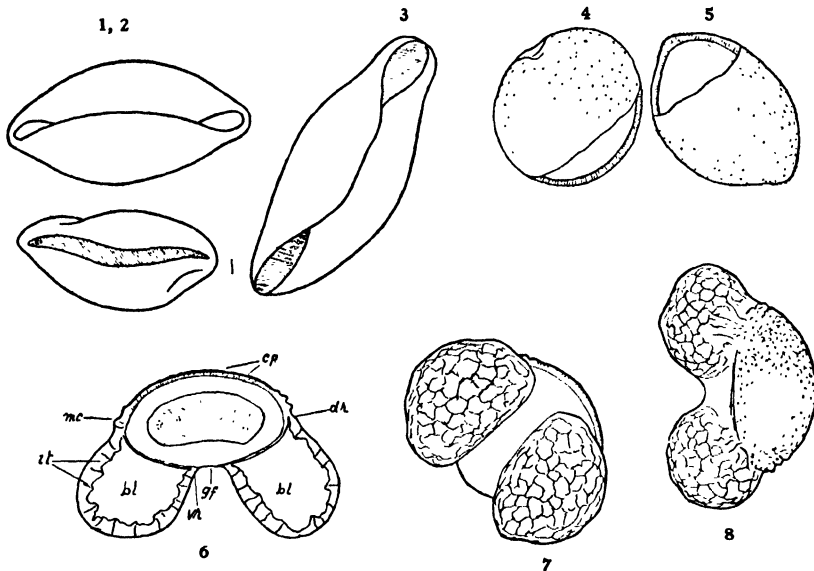
ABIETINEAE

Wherever fossil pollen grains are found those of the Abietineae are generally the most conspicuous and often the most numerous. They have been recorded in the earliest of the Lower Cretaceous floras known from Europe, of the Wealden age, by Graf. Solms-Laubach in his *Pytisporites* sp. from Franz Joseph Land, and by Nathorst in his *Pytisporites* sp. from Scania. And all through the paleobotanical literature of succeeding ages the scattered references to pollen grains that are encountered from time to time generally are concerned with the large and conspicuous winged grains of the Abietineae.

Though it is the winged grains of the Abietineae that have been observed most frequently, not all of the Abietineae have winged grains. As a

matter of fact, on the basis of their pollen morphology the Abietineae may be divided into two groups, the *winged-grained* and the *wingless-grained*. To the former belong *Pinus*, *Picea*, *Abies*, *Cedrus* and *Pseudolarix*; to the latter belong *Tsuga*, *Larix*, and *Pseudotsuga*. The pollen grains of these two classes are remarkably distinct and there are no intermediate forms among living species.

The grains of the winged-grained group are characterized by the possession of two large and conspicuous air-filled bladders (fig. 7), one on



Figs. 1-3, *Cycadopites*. Pollen grains probably of various Cycads, fig. 1, pollen, 45μ long, fig. 2, 26μ long, fig. 3, 37μ long; figs. 4, 5, *Dioonipites*, fig. 4, 30.4μ , fig. 5, 33μ in diameter, fig. 6, optical section, diagrammatic, of a grain of *Pinus*; fig. 7, *Pinus strobilipites* seen from the ventral side; fig. 8, *Pinus scopulipites*, end view.

All figures were drawn from studies made at a magnification of 900, using a Zeiss 3 mm. apochromatic objective, N. A. 1.4, and paired $15\times$ binocular eyepieces. Measurements, excepting those of very large grains, were made at a magnification of 1800, using a 2 mm. apochromatic objective, N. A. 1.3, and a $20\times$ eyepiece. The sizes of the drawings are chosen to best display the characters of the grains and do not bear a constant relation to their dimensions.

each side of the germinal furrow. On this account such a grain possesses bilatical symmetry, and dorsal and ventral sides are differentiated. The ventral (the lower in fig. 6) bears the single germinal furrow (g.f. fig. 6), which extends from end to end of the grain, vertically to the plane of the diagram. It is not sharply defined, consisting merely of a longitudinal strip of thin flexible exine between the two bladders (bl) which flank it on either

side. The bladders are large balloon-like structures which, when the grains are moist and expanded, stand out wing-fashion; hence they are sometimes called wings. They are attached along the margin of the furrow by their ventral roots (vr) and above by their dorsal roots (dr). The dorsal surface of the grain is covered with a layer of very thick and more or less rigid exine, the cap (cp) or disc. The texture of this is peculiar and highly distinctive. It has the appearance of being composed of two or more substances twisted and rolled together, and towards the margin of the cap it is thrown into upstanding convolutions which surround the cap more or less completely as a frill-like projecting rim, the marginal crest (mc). Immediately below the marginal crest the exine of the cap merges into the dorsal roots of the bladders which are morphologically only tangential splits in the thickened exine. In the bladders the curious convolutions of the texture of the cap are carried by the outer wall and are thrown into inwardly projecting ridges, the internal thickenings (it) which lend a stiffening effect to the outer walls of the bladders. When such a grain dries and shrinks the furrow is drawn inwards and upwards, a movement which causes the bladders to become closely appressed to each other forming an effective closure for the furrow, the protection of which is their obvious function.

The grains of the living species of the winged-grained Abietineae bear a remarkably close resemblance to one another, differing principally in their size, the relative size and shape of their bladders, and such less conspicuous characters as the thickness and roughness of the exine of the cap and the degree of development of its marginal crest. In size the grains of the living species which I have observed of *Pinus*, *Pseudolarix* and *Cedrus* range from 48 to 64 μ in diameter, exclusive of the bladders, while those of *Picea* range from 68 to 85 μ , and those of *Abies* 85–109 μ . Measurements of these grains must always be made exclusive of the bladders because the condition of the grain (i.e. the degree of its expansion) at the time of its observation determines the width of separation of its bladders. The grains of *Pinus* and *Pseudolarix* are further characterized by the shape of their bladders which tend to be globular and do not become concaved, or only slightly so, on their proximal surfaces when they are dried and contracted, while the bladders of the grains of *Cedrus*, *Picea* and *Abies* may become decidedly concave as the grains contract.

The grains of the WINGLESS-GRAINED ABIETINEAE cannot be so generally characterized, those of each genus presenting its own peculiar characteristics. Accordingly their further discussion is deferred to the consideration of the various genera.

In the Green River oil shales the grains of the WINGED-GRAINED

ABIETINEAE are the most conspicuous elements, and their preservation is almost perfect. On the basis of their size they fall into three groups, apparently representing the three genera *Pinus*, *Picea* and *Abies*, and a single specimen which conforms more closely to the pollen of *Cedrus*.

Pinus

The numerous grains of the smaller size group (viz. 48–65 μ), which are undoubtedly those of *Pinus*, show a rather wide variation in their individual sizes and the degree of development of their marginal crests (figs. 7–9). So much is this so that it is certain that these grains represent more than a single species. On the basis of their size alone they fall into three classes. Accordingly these are provisionally regarded as species. Moreover it is quite possible that each of these provisional species represents more than a single natural species because the grains of different living species of *Pinus* are frequently virtually identical in size as well as in their other characters.

Fossil grains of *Pinus* occur almost wherever fossil pollen is found. They have been recorded from European Eocene and Miocene brown coals (24, 41), and their existence in the Green River shales has already been pointed out (16). Here they occur in enormous numbers; they are the most numerous of all the conifers and among the most numerous pollen grains of any kind. Yet no species of pine is otherwise represented in the Green River flora. Pines are known to have existed since Cretaceous times, and throughout the Tertiary were rather widespread, yet they are not nearly so well represented in the known fossil record as some other conifers such as *Taxodium*, *Tumion* and *Sequoia*. The pollen record of the oil shales suggests that this disparity between the abundance of the fossil pollen and other records of the trees is due to the fact that the pines were upland species not favorably situated for fossilization except through their pollen.

***Pinus strobipites* sp. nov.** (fig. 7). Grains essentially the same as those of the living *Pinus Strobis*, measured across the disc, exclusive of the bladders, 47.9–52 μ . Marginal rim marked by a slightly roughened thickening of varying extent. Bladders about 43–46 μ in diameter, generally inclined to be globular, but their size, shape, and position, relative to the body of the grain, depending largely upon the degree of its expansion. *Holotype*: 36–20.0–61.5.

These grains are exceedingly abundant in the shales and very uniform, possibly all representing a single species which may have been the same as, or closely related to *Pinus Strobis*, though, as far as the evidence of its grains indicates, it might have been just as closely related to *P. nigra* or *P. attenuata*.

Pinus scopulipites sp. nov. (fig. 8). Grains essentially like those of the living *P. scopulorum*, differing only in the slightly lesser development of the marginal crest, 54–60 μ in diameter. *Holotype*: 6–11.25–62.5.

These grains are somewhat less numerous in the shales, than the preceding species. Eight perfectly preserved specimens were examined in detail, and many, less favorably preserved, were observed. One of the outstanding characters, other than that of size, which seems to distinguish this species from the preceding, is the superior development of the marginal crest.

Pinus tuberculipites sp. nov. (fig. 9). Grains essentially like those of *P. tuberculata*, 64–65 μ in diameter. Cap approximately circular or squarish in outline, marginal crest well developed, particularly in the regions above the ends of the furrows. *Holotype*: 8–13.4–59.2.

Six well preserved specimens were observed. These are all alike except for the size and shape of their bladders; in one specimen they are relatively large and puffy, while in another they are smaller than is usual with grains of *Pinus*. It is likely, therefore, that the different specimens brought together under the present name represent two or three natural species.

Picea

The grains of the living species of *Picea* are similar to those of *Pinus*, except for their larger size. The three species which I have examined range from 68–86 μ in diameter, exclusive of the bladders. The bladders also have a tendency to be flattened dorsiventrally, giving them a pointed appearance when the grain is observed in end view, and as they are pressed together upon drying they may even become concaved over the whole of their proximal surfaces.

Picea grandivescipites sp. nov. As in the generic description (fig. 10).

These are much less numerous than grains of *Pinus*. I was able to find only six specimens that were in a satisfactory state of preservation; they are not all alike and certainly do not all belong to the same natural species, for the smallest measures 70 μ in diameter and the largest 85 μ . In four of the specimens the bladders are large and puffy, resembling those of the grains of *Pinus*, while in the other two they are smaller and greatly compressed dorsiventrally. These differences in the forms of the bladders, however, are not reliable criteria, and without a larger number of specimens, can have little diagnostic value. They are less significant than the variation in size which alone suggests that the six specimens represent two or three natural species. *Holotype*: 4–6.4–70.4.

Picea is represented in the Green River formation by the single species *Picea pinifructus* R. W. Brn. based on a winged seed. Recognizable fossils of *Picea* are extremely rare throughout the Tertiary formations, but this is probably due to the fact that the trees grew in environments mostly unfavorable to fossilization. Their pollen in the oil shales suggests that they were rather abundant. *Picea-pollenites alatus* Pot. is described from Miocene brown coals of Europe.

Abies

The pollen grains of the living species of *Abies* differ from those of the other winged-grained Abietinae in their larger size. The two living species which I have examined measure about 95 and 107 μ in diameter respectively, exclusive of the bladders, and both are characterized by the proportionately much smaller size and more globular shape of their bladders than the grains of either *Pinus* or *Picea*.

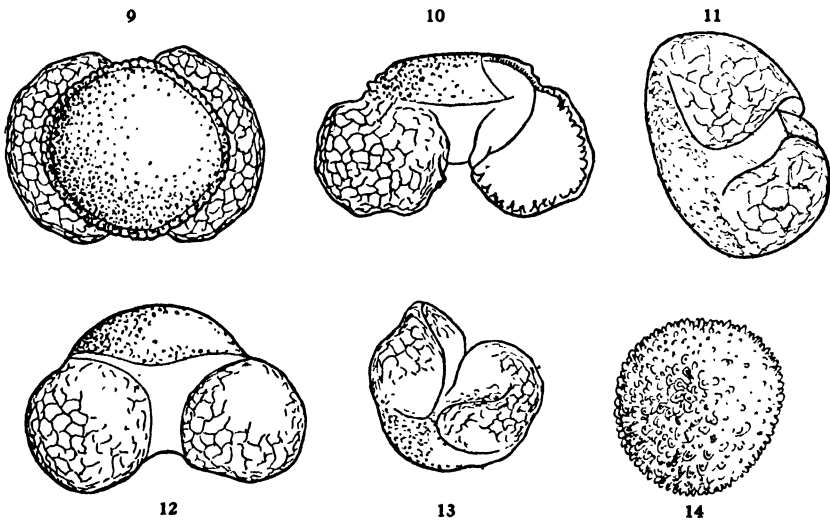


Fig. 9, *Pinus tuberculipites*, dorsal view; fig. 10, *Picea grandivescipites*, end view; fig. 11, *Abies* sp.; fig. 12, *Abies concoloripites*, seen ventrally and from one end; fig. 13, *Cedripites eocenicus*, seen ventrally and from one end; fig. 14, *Tsuga viridi-fluminiipites*.

Six specimens which appear to belong to this genus were found in the oil shales. Only the two described below and which are apparently both of the same species, however, could be closely matched with any living species. Of the other four specimens two measure 104 μ in diameter; in one of these the bladders are expanded, in the other they are closely appressed against the ventral face of the grain (fig. 11). Another grain measures 143 μ in diameter and has bladders large and puffy similar to those of

the grains of *Pinus*. Another measures 140μ in diameter and has only rudimentary bladders. This latter specimen is too poorly preserved to warrant describing it in detail, but its large size, in association with exceedingly weakly developed bladders, suggests that it may represent a primitive member of the Abietineae of a type that is now extinct. These four specimens probably represent four natural species, which either belong to the genus *Abies* or to a closely related genus which no longer exists.

Fossil firs have not heretofore been recorded from the Green River formation and are of extremely rare occurrence in the Tertiary. The presence of these grains, though relatively few, indicates that firs must have been fairly abundant during the Green River epoch for the size of their grains is certainly large enough to seriously impede their dispersal by wind, and would therefore, be expected to greatly reduce their representation in the shales.

***Abies concolipites* sp. nov.** (fig. 12). Grains about $90\text{--}110\mu$ in diameter, corresponding in almost all observable characters to those of *Abies concolor*. Body of the grain, in its expanded condition, ellipsoidal or nearly spheroidal in form, bearing two nearly globular bladders. Exine of the cap rather thick and finely granular, its texture passing abruptly into the smooth texture of the ventral surface, but with no suggestion of a marginal crest. *Holotype*: 8-13.6-59.5.

Only two grains of this species were found, but they are in an excellent state of preservation, and I feel that their identification with *Abies* is certain.

***Cedripites* gen. nov.**

Essentially like the grains of *Cedrus Libani*, similar to those of *Pinus*, measuring about $51\text{--}56\mu$ in diameter, exclusive of the bladders, but distinguished from the grains of *Pinus* by their proportionately larger bladders which are decidedly concave on their proximal faces, so that if not fully turgid, they have the appearance of closing about the grain somewhat like the two sides of an overcoat, that is too large for the wearer, drawn loosely about the body.

Among the Green River shales was found a single specimen answering this description. The identification of this with the genus *Cedrus*, is of course only problematical, though its peculiar form is not shared with the grain of any other member of the winged-grained Abietineae.

***Cedripites eocenicus* sp. nov.** (fig. 13). Cap 46μ in diameter. Exine rather thick, finely reticulate-granular. Bladders large and flaccid, loosely enveloping the ventral surface of the grain. *Holotype*: 8-7.1-65.6.

Cedrus has not been previously recorded from the Green River formation, nor, as far as I am aware, anywhere in Tertiary deposits. It is, however, known to occur in the Lower Cretaceous of Maryland and its present distribution in Central Asia and North Africa suggests that, like many other Asiatic trees, it may have been one of the American groups that were driven out by the Pleistocene glaciation but was never able to return.

Tsuga viridi-fluminipites sp. nov. (fig. 14). Apparently nearly spherical in life, 78μ in diameter, though in the single specimen found it is flattened in the plane of the section. The entire visible surface of the exine is thick and rather uniformly deeply convolute, giving it a coarsely pebbled appearance. Furrow and bladders entirely lacking. *Holotype*: 6-17.7-64.0.

The size of the grain and the character of its convolutions correspond exactly with the grains of *Tsuga canadensis*. If it could be proved that the lower surface of this grain is similar to the upper—and there is no reason to suppose that it is not—its identification with *Tsuga* would be practically certain. Lacking a knowledge of the under side, however, this specimen might be confused with some fern spore which has a triradial crest on one side, or with some one-furrowed grain of the Abietineae.

Tsuga has not before been recorded from the Green River formation, nor elsewhere in the Eocene. It does, however, occur in the Miocene Latah formation (9). And its present distribution through temperate North America, Japan, central and southwestern China and the Himalayas suggests that it was probably present in America during the Green River epoch.

Abietipites gen. nov.

Intermediate in form between the grains of *Pinus* and *Tsuga*, provided with a single clearly defined furrow, and a single weakly developed bladder encircling the grain.

This genus is provisionally established to receive species of pollen which appear to belong to the winged-grained Abietineae but do not correspond to any living genus.

Abietipites antiquus sp. nov. (figs. 15, 16). Grains in life apparently lens-shaped or spheroidal, though such is a deduction rather than a statement of fact for the two specimens upon which this description is based are greatly flattened dorsiventrally. Exine of the dorsal surface crinkly granular, exactly like that of *Pinus*, towards the margin of the cap becoming loose in structure and somewhat puffy, and extending beyond the body of the grain as a frill which completely encircles its perimeter. This marginal frill merges with the exine of the ventral surface which is of a loose structure like that of *Tsuga*;

grain provided with a single clearly marked long ventral furrow, more or less tapering, reaching almost or completely across it. *Holotype*: 8-6.4-63.7.

One of the specimens is seen in ventral view (fig. 15) and the other in dorsal view (fig. 16), and both are transparent so that their lower as well as the upper surfaces can be seen. There is considerable difference between the two specimens. The former measures 50.2μ over all and 36.5μ inside the marginal frill (fig. 15), while the latter measures 70μ over all and 45.6μ inside the marginal frill (fig. 16). In the former the furrow tapers at both ends and is not quite as long as the grain, while in the latter it is fully as long as the grain with both ends broad. In the former the encircling frill is of uniform width around the grain while in the latter it is deeply notched in the regions of the ends of the furrows. Though these differences are great enough to make it appear that these two specimens may represent two natural species, the two grains are certainly closely related.

The frill of puffy exine can only be interpreted as a rudimentary bladder. Such structures are common among the spores of various groups as the Pteridosperms, Caytoniales (43) and Pteridophytes, but as far as I am aware, are never found in these groups in association with such a well developed furrow. These specimens appear, therefore, to represent a primitive form of the winged-grained Abietineae. The remarkable resemblance of the texture of its ventral surface to that of the pollen grain of *Tsuga*, among the wingless-grained Abietineae, and of its dorsal surface to that of the grains of the winged-grained Abietineae give it an intermediate position between the winged and wingless-grained groups, and is strongly suggestive of the way in which one of the forms might have been derived from the other.

CUPRESSINEAE, TAXODINEAE AND TAXINEAE

The grains of the living representatives of these three coniferous tribes are alike in many respects, and are at once distinguished from those of the other tribes of the Coniferae by their thin and flexible exine and extremely thick intine. The exine, though always thin, is somewhat various in this respect in the different species. It is always flecked with fine granules; in some the granules are numerous and closely packed; in others they are few, generally irregularly grouped, leaving rather large patches of the exine bare, and often they are easily detachable. The intine which is always of remarkable thickness, is of a hyaline material with a large capacity for absorbing water which causes it to swell enormously, generally with the rupture of the exine, excepting in those grains of which the latter is too thick. The way in which the exine ruptures is a diagnostic character of value, particularly in fossil material where only cast exines are found.

The grains of this plexus of tribes also possess certain characters which serve in living material to distinguish the tribes from each other. In those of the Cupressinae there is never a germ pore or furrow, only occasionally may a vestige of this organ be found. On the other hand among the Taxodineae and Taxineae the germinal furrow is always represented by at least a vestige which, though small, is generally quite conspicuous. In the grains of the Taxodineae it takes the form of a vertically elongate straight or bent papilla, while among the Taxineae it is a broad and meridionally elongate protuberance. Unfortunately, however, in fossil material, the presence or absence of the pore, or furrow vestige, is seldom visible in those grains which rupture easily, for the break generally takes place through the pore. One must, therefore, generally rely for the identification of these upon such characters as the dimensions, the mode of rupture of the exine and the number and distribution of the granular flecks over its surface, characters which make identification, closer to one than another of the three tribes, somewhat uncertain.

In the oil shales are many grains answering the above description making it quite certain that members of one or the other, or possibly all three tribes of this plexus were exceedingly abundant in Green River time. Relatively few of the grains, however, are sufficiently well preserved to reveal the minute and intangible differences existing between those of the different genera. But among them the following can be distinguished with a fair degree of certainty.

Taxodium hiatipites sp. nov. (fig. 17). The split and empty exines of grains which seem in all probability to be those of a species of *Taxodium*. The cleft generally bisects the grain almost completely, but the two halves remain joined at their bases, and opening generally without much buckling though sometimes one of the halves may be crumpled. In size, measured from the tip to the base of one of the halves where it remains joined to its neighboring half, 29.6–37.6 μ . *Holotype*: 5–12.6–51.6.

All of the various conditions in which I have found these skins could be exactly matched with the pollen of the living *Taxodium distichum*. The number and arrangement of the surface flecks also match perfectly. There is nevertheless a possibility that these grains might be those of *Juniperus communis* (they are too large for any other species of *Juniperus*) or of *Libocedrus*, though they do not match either quite so well as they do those of *Taxodium*. They are among the most conspicuous pollen elements of the shales; scores of them occur in the sections which I have examined.

Besides the flecked grains there are a few which are quite smooth but otherwise answer the above description. Since it is easily demonstrable

that the flecks of the exine surface are detachable, I am including these grains with the present species on the assumption that they are *Taxodium* grains that have lost their flecks. On the other hand if these grains never had flecks they cannot belong to *Taxodium*. Instead they would match rather well with those of *Thuja* which are only sparsely flecked, or with the grains of some species of *Zamia*, which rupture in this fashion, and are quite smooth. However, bereft of their flecks, grains of this type are reduced to such simplicity that it is without profit to attempt their identification.

A similar grain which I suspect is of the same, or a closely related, species is described as *Pollenites hiatus* Pot. from European Miocene brown coal (41). The name of the present species has reference to the gaping appearance of these empty exines, as suggested by Potonié's name for a similar, if not the same, species.

Taxodium has not been recorded in the Green River flora, unless, perchance the leaves of *Taxites eocenica* R. W. Brn., which Brown (17) states "are suggestive of such coniferous genera as *Taxus*, *Taxodium*, *Tumion*, *Abies*, and *Pseudotsuga*," are to be regarded as such. *Taxodium* belongs, however, to an immensely ancient group whose record dates back to the Cretaceous period. "There are no certainly identified records of ancestral bald cypress in the Cretaceous period, although it is quite possible that some of the similar appearing twigs of fossil conifers that have been referred to *Sequoia* may really be those of an early Cypress." (5). *Taxodium* was of wide distribution in Tertiary times, and is recorded from the Greenland, Wilcox, Fort Union, Jackson and other floras of that period, and in Asia from the Sarmatian flora of Krynka River (35). It is represented in the southern part of North America at the present time by two species, one of which reaches as far north as Maryland. Consequently its presence in the Green River epoch is to be expected.

Glyptostrobus vacuipites sp. nov. (fig. 18). The cast skins of pollen grains, split into two approximately equal halves. Exine in life apparently stiff and under mechanical strain so that, in separating, the two halves buckle with the formation of longitudinal folds. Outer surface dotted with small flecks openly and irregularly spaced. Length of halves 37.6μ . *Holotype*: 5-12.6-50.5.

This grain matches the pollen grains of the living *Glyptostrobus*, which upon rupturing frequently assume this form; they are of almost exactly the same size, and the distribution of the flecks on their surface is likewise the same. It must be admitted, however, that the fossil shows no characters which entirely exclude the possibility of its belonging to some of the other members of this plexus of tribes.

Glyptostrobus, now confined to a small region in central China, belongs to the same ancient group as *Taxodium*. It was wide spread throughout the Tertiary period, and is recorded in the Tertiary Claiborne, Jackson, Wilcox and British Columbia floras, consequently it may be expected in the Green River epoch, though it has not been previously recorded. What has been said regarding the past distribution of *Taxodium* applies equally here, for much of what has been called *Sequoia* appears to be *Glyptostrobus*.

Cunninghamia concedipites sp. nov. (fig. 19). Empty but unruptured exines of pollen grains, 32–37 μ in diameter, thin and collapsing irregularly without predetermined folds. Outer surface covered with minute flecks closely but irregularly packed, or smooth. With or without a small rounded papilla. *Holotype*: 5–11.1–52.8.

Six grains were found answering this description, and they match very well with those of the living *Cunninghamia sinensis*. Four of them possess the flecked character of the group and two are quite smooth, but surrounding one of the latter is seen a halo of small granules which had apparently been stripped from the exine. In both of the smooth grains could be seen a minute papilla corresponding to that of the grains of *Cunninghamia*, but in the others no papilla was apparent. But its absence cannot be inferred, for in the collapsed grains of living species of *Cunninghamia* the pore is generally not visible.

The large size of these grains (all except one are over 34 μ in diameter) is a character of the *Taxodineae* and precludes the likelihood of these specimens belonging to any of the *Cupressineae*, for those which I have examined are all under that size. The rather coarse nature of the exine and its mode of collapsing without rupture is quite characteristic of the grains of *Cunninghamia*, so that it is with a high degree of confidence that these grains are assigned to that genus. The specific name of these grains has reference to their customarily collapsed form.

Cunninghamia has not been recorded from the Green River formation, nor elsewhere in the Tertiary, so far as I am aware, but one species, *C. elegans* Corda is recorded from the Upper Cretaceous (3).

GNETACEAE

Ephedra eocenipites sp. nov. (fig. 20). Ellipsoidal, 57–74 μ long and about one-half as broad, bearing 5–7 high vertical ridges extending almost from end to end. The grooves between the ridges are each traversed throughout their length by a zigzag hyaline line giving off from its angles short branches which pass outwards into the ridges. Exine thick, smooth and of a horny appearance. *Holotype*: 5–14.65–49.8.

These grains are rather numerous in the oil shales. Six were encountered in an excellent state of preservation and about as many more in a less favorable condition. They correspond in every detail, except their somewhat larger size, with the grains of such living species as *Ephedra glauca* which is about 47μ long, *E. equisetina* Bunge, 53μ , and *E. viridis* Coville, 53μ . In size the six fossil species which were measured are 57, 60, 64.5, 65.6, 68.4 and 74μ long.

The grains of the living species of *Ephedra* are of two types, those with about fifteen low ridges and no hyaline lines in the grooves between them, and those with about five to seven high ridges with distinct hyaline lines in the grooves. It is to this latter type that the fossils all correspond. The size of the grains of any one of the living species is almost constant. The rather great range in size of the fossil specimens, therefore, makes it certain that two or three natural species are involved, and probably none of them is exactly the same as any of the living species. Nevertheless the identity of these with the genus *Ephedra* is rendered certain by their odd and extremely characteristic shape which is not found elsewhere among pollen grains or spores.

Ephedra has not been previously recorded from the Green River formation, nor from the Eocene of America, though it has undoubtedly long been an inhabitant of this continent. But the late Dr. A. H. Hollick had in his possession, shortly before his death, a specimen from the Miocene Florissant which appears to be a fragment of a plant of *Ephedra*, though he had not positively identified it as such. At present the genus is represented in America by six species of low desert shrubs, and at least four of these are found growing in the immediate vicinity of the Green River formation. The majority of the species are now Asiatic, a fact which is strongly suggestive of their American existence during Tertiary time.

NAJADACEAE

Potamogeton Hollickipites sp. nov. (fig. 21). Spheroidal, somewhat ellipsoidal, ovoidal or variously irregular, $16-27.4\mu$ in diameter. Exine rather thin and conspicuously reticulate with a coarse network of beaded ridges. Without pores or furrows, or vestiges of them. *Holotype*: 3-7.9-43.7.

These grains are fairly common in the oil shales; ten perfectly preserved specimens were found and examined in detail. Besides these ten grains there are a number of others of which less than the whole surface can be seen; therefore, it is not known for certain whether they have a germ pore or not, the absence of which is the only character which distinguishes these grains from those of *Sparganium* and some species of *Typha*; but I do not feel that any of these belong to the *Typhaceae*, for

the latter produce pollen in enormously larger quantities than the *Najada-ceae* and would therefore be expected to greatly outnumber them in the shales, if the plants had been present.

Potamogeton has not been previously recorded from the Green River formation, but it is represented in the Eocene Wilcox (10), Jackson (6), Miocene Latah (29) and Florissant (26, 18) floras, and, since the latter is regarded as a derivative of the Green River flora, it is to be expected that *Potamogeton* lived during the Green River epoch. It is known to have occurred in the Tertiary Siberian flora (32), and in the Tertiary Samartan flora of Krynka River (35), so its presence in the oil shales points to the northern connections of the Green River flora.

The habits of *Potamogeton* are similar to those of *Myriophyllum* (q.v.), and the presence in the oil shale of its pollen which appears to be mainly insect borne and not likely to be carried far from its point of origin, is interesting in suggesting the nature of the conditions under which the shales were deposited.

The specific name of the present species is in honor of the late Arthur Hollick, Paleobotanist.

ARECACEAE

Arecipites gen. nov.

Ellipsoidal, 23–25 μ long, with a single longitudinal furrow which may close tightly throughout its entire length, not gaping at its ends. In form and structure resembling the grains of *Phoenix dactylifera* (44).

It is with some hesitation that these grains are referred to the Palm family on account of the widespread distribution among primitive floras of species with one-furrowed grains of this general character, with which they might be confused. Of such a character are the grains of the Magnoliaceae, Cycads, *Ginkgo* and Bennettitales, but, as far as my experience goes with such forms, the small size of these fossil grains precludes the possibility of their belonging to the Magnoliaceae, and the pointed ends of their furrows do not match the broad rounded ends of those of the Cycads, *Ginkgo* or the Bennettitales.

Four species or Arecaceae have been recorded from the Green River formation (11, 27), and they are known to have grown in great profusion in many regions throughout the Tertiary period.

Arecipites punctatus sp. nov. (fig. 22). Exine minutely pitted but appearing, except under the most favorable conditions, to be quite smooth.

The single specimen which was found matches the grains of *Phoenix dactylifera* in every respect except its somewhat larger size,—the latter range from 19.4–23.9 μ in length. *Holotype*: 8–11.0–61.4.

Arecipites rugosus sp. nov. (fig. 23). As in the generic description, except that the exine is decidedly roughened and appears to have transverse striae. *Holotype*: 36-8.0-58.6.

A single specimen of this species was observed. The furrow is deeply invaginated, and its floor may be seen through the transparent exine, though its margins are pressed tightly together. This grain, in size and structure, corresponds with those of the Arecaceae, but in texture does not correspond with any species with which I am familiar. It is therefore somewhat doubtful if it is correctly assigned to the family.

ARACEAE

Peltandripites gen. nov.

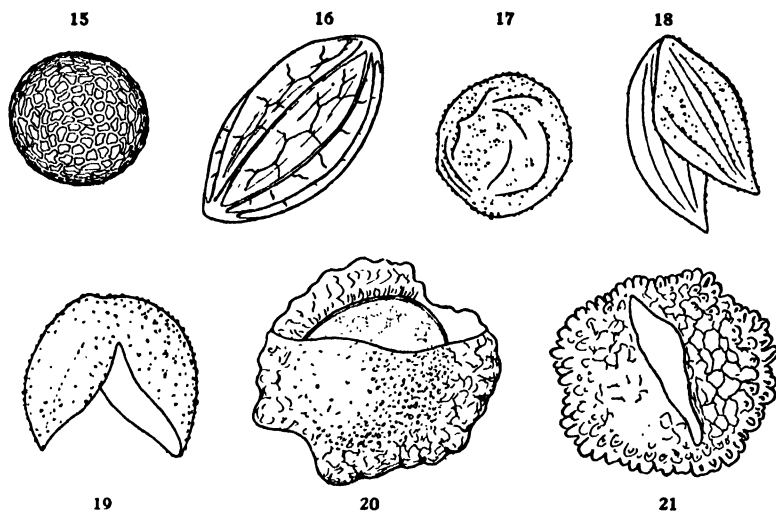
Ellipsoidal, without germinal furrows or pores. Exine rather thin and of smooth texture, but provided with numerous sharp conical spines somewhat irregularly arranged, often obliquely attached and of varying length. As seen in optical section the exine appears to be slightly roughened on its inner surface.

Peltandripites Davisii sp. nov. (fig. 24). $40 \times 35.3\mu$. Spines averaging about 2.3μ long. *Holotype*: 4-10.0-61.6.

A single specimen of this species was found. It matches with the grains of *Peltandra virginica* Kunth, except for its slightly larger size and slightly more numerous spines. The grains of the latter species are $30-35.3\mu$ in diameter; their spines are of the same size and general appearance as those of the fossil species, though less numerous and more regularly arranged. In these two latter characters the fossil species is intermediate between the grains of *Peltandra* and *Smilax herbacea*, the only other species with which it compares at all closely. The fossil species, however, is much larger than the grains of *S. herbacea* and its spines longer.

Peltandra has not been previously recorded from the Green River formation nor elsewhere in fossil form as far as I am aware, but the Araceae are represented in the Tertiary by *Acoris* in the Florissant and Wilcox floras, by *Pistia* in the Wilcox and Jackson, and by *Arisaema* in the Latah. I feel that the assignment of this grain to the Araceae is certainly correct, but its identification with *Peltandra* is not entirely certain for I have not had opportunity to compare it with many other members of the family. It does not, however, match with the pollen of *Symplocarpus*, *Anthurium*, *Calla* or *Arisaema*.

The specific name of the present fossil species is in honor of Charles A. Davis who prepared most of the slides upon which this work was done, but whose untimely death in 1916 prevented him from studying them.



Figs. 15, 16, *Abietipites antiquus*, fig. 15, ventral view of a grain 50.2μ over all, fig. 16, dorsal view of a grain drawn as if part of the surface were removed to show its appearance in optical section, 70μ over all; fig. 17, *Taxodium hiatipites*; fig. 18, *Glyptos-trobis vacuipites*; fig. 19, *Cunninghamia concedipites*; fig. 20, *Ephedra eocenipites*; fig. 21, *Potamogeton Hollickipites*.

LILIACEAE

Smilacipites gen. nov.

Spherical or ellipsoidal, $19-25.8\mu$ in diameter, without a germ pore or furrow. Exine rather thin and; in life, apparently readily deformed by pressure; variously adorned, provided with large or small spines or wart-like granules, texture smooth or only faintly granular.

I have compared these fossils with the pollen of three living species of *Smilax*. The grains of the latter are all spherical, thin walled and variously adorned. That of *S. herbacea* L. is $25-27\mu$ in diameter and provided with sharp conical spines, that of *S. populnea* Kunth, is about $19-20\mu$ in diameter, provided with large wart-like protuberances, and that of *S. mollis* Willd. is about 17μ in diameter, and provided with small papillae. There is much variation in the size and development of the surface adornments even among the grains of the same species and they are always irregular in arrangement. The texture of the exine is otherwise quite smooth.

Though at least one of the fossil species matches perfectly with one of the present day species of *Smilax*, it is not entirely safe to assign any of these fossils unreservedly to the genus *Smilax*, for the same form of grain is known to occur in a number of other groups. For example it is almost exactly duplicated in the Araceae, and, except for size, in *Gnetum*, and is rather closely approached in the Lauraceae and Musaceae.

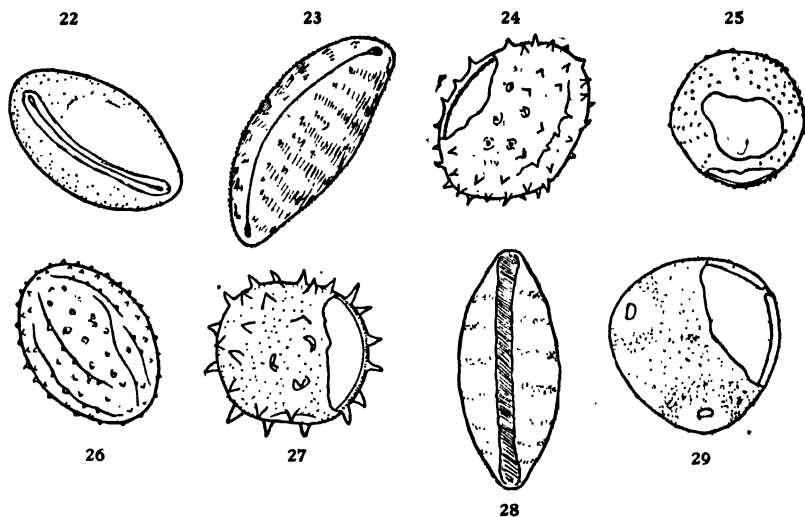


Fig. 22, *Arecipites punctatus*; fig. 23, *Arecipites rugosus*; fig. 24, *Peltandripites Davisii*, drawn as if part were removed to show its appearance in optical section; fig. 25, *Smilacipites molloides*, the upper part of the grain has been sliced off by the microtome, and the remainder is drawn as if a piece were removed from one side to show its appearance in optical section; fig. 26, *Smilacipites herbaceoides*; fig. 27, *Smilacipites echinatus*, drawn as if a part were removed from one side to show its appearance in optical section; fig. 28, *Liriodendron psilopites*, ventral view; fig. 29, *Hicoria viridi-fluminipites*, ventral view, drawn as if a part were removed, to show its appearance in optical section.

Smilax has not previously been recorded from the Green River formation, but one species is found in the Eocene of the Atlantic Coastal Plain, and another from the Tertiary Samartan flora of Krynka River (35), and many are recorded from the Cretaceous to Pliocene of other regions. (6, 9, 10).

***Smilacipites molloides* sp. nov.** (fig. 25). As in the generic description, 19.4μ in diameter. Exine papillate, but texture otherwise smooth. Single specimen found matches exactly with *Smilax mollis* from which its specific name is derived. *Holotype*: 3-8.7-41.6.

***Smilacipites herbaceoides* sp. nov.** (fig. 26). Ellipsoidal, 27.4μ long, but the exine is wrinkled so that the grain was probably less ellipsoidal in life. Provided with small irregularly arranged sharp spines. *Holotype*: 8-11.9-63.6.

This specimen differs from the grains of *S. herbacea* only in its elongate form and smaller spines. The only other genus that this might belong to is *Peltandra*. In the latter, however, the spines are more regularly arranged and the exine is a little thicker.

***Smilacipites echinatus* sp. nov.** (fig. 27). Spheroidal or approximately so, 28.5μ in diameter. Exine rather heavy, finely and vaguely granular, or smooth,

provided with long sharp spines irregularly arranged, averaging about 3.4μ in length. *Holotype*: 3-7.8-42.8.

The spines of this species are more pronounced than is usually the case with grains of *Smilax*. It is to this fact that the specific name refers. Two specimens were found. One of these shows the granular character rather distinctly while in the other it is absent. If the granular character is natural, as it appears to be in one of the specimens, it would preclude the possibility of its belonging to the genus *Smilax*.

MAGNOLIACEAE

Liriodendron psilopites sp. nov. (fig. 28). Ellipsoidal, $62.5 \times 23.5-80 \times 38.8\mu$, provided with a single longitudinal furrow. In the partially expanded condition the furrow is rather broad, of uniform width, not tapering towards its ends, its margins slightly wavy. Exine rather thick and apparently rigid in life, of smooth texture but slightly undulating. It is to the smooth texture of these grains that the specific name refers. *Holotype*: 17-11.9-69.5.

Three specimens of this species were found, and the one that is seen to best advantage (i.e. in ventral view showing the furrow) matches the grain of the living *Liriodendron Tulipifera* in every character except the texture of its exine. In the grains of the living species the exine presents a minutely pitted and somewhat warty appearance. In the grains of other living Magnoliaceae, however, such characters are only of specific value, both smooth and rough grains being found in the same genus. It seems most likely, therefore, that the present fossil is the grain of an extinct species of *Liriodendron*. There is also a possibility, however, that it might belong to some member of the Magnoliaceae that I have not examined, or even to some species entirely unrelated, for one-furrowed grains were much more common among the primitive floras than they are today.

Liriodendron is known to have occurred in the Upper Cretaceous and several species have been recorded from the Eocene (8, 36) and the Miocene (9) formations, consequently it is to be expected in the Green River epoch.

JUGLANDACEAE

Pollen grains of the Juglandaceae are abundant and among the most conspicuous in the oil shales. But owing to the exceptionally wide range of form embraced by the pollen of the various genera of this family, they are not easily identifiable, excepting the conspicuous grains of *Hicoria* and *Juglans*. Consequently, in order that the identifications may be fairly evaluated, I give the following short summary of the pollen characters of

some living Juglandaceae which are likely to be represented in Tertiary formations.

The characters which they share with each other are the smooth or slightly granular character of their exine, their lack of germinal furrows, and their possession of rounded or slightly elongate germinal apertures always surrounded by subexineous thickenings. In the grains of all, except *Hicoria* and *Juglans*, the pores are approximately equally spaced around the equator as in the grains of the Betulaceae, but in the grains of *Hicoria* and *Juglans* the pores are mostly crowded into one hemisphere (the ventral) leaving the greater part of the other (the dorsal) blank. Also in the grains of these two genera the subexineous thickenings of the pores possess but little thickness and do not cause the pores to protrude noticeably above the surface of the grain; instead, they possess greater lateral extension. In the grains of most species of *Juglans* the subexineous thickenings do not quite touch each other, but in those of *Hicoria* they not only touch but are completely fused, forming a continuous sheet underlying the exine of the whole of the ventral hemisphere and all but a small central area of the dorsal hemisphere. On account of these two characters, the one-sided arrangement of their pores and their broad flat subexineous thickenings surrounding them, the grains of *Hicoria* and *Juglans* are easily recognizable. Not so, however, with the grains of such other genera as *Engelhardtia*, *Pterocarya* and *Platycarya*; their pores are arranged around the equator, their subexineous thickenings are abrupt and their pores protrude as in the grains of the Betulaceae which they resemble closely, and, to a lesser extent, some of the Urticaceae, such as *Momisia*; and indeed it is often difficult to distinguish the grains of these families one from the other except through a knowledge of their specific characteristics. The grains of *Pterocarya* range from about 27–36 μ in diameter. They are rather distinctive in usually having five or six pores, rarely four, and almost never three. The pores are narrowly elliptical in shape and arranged around the equator with their major axes converging in pairs. They resemble the five-pored grains of *Alnus* in almost all respects except that they lack the connecting bands which characterize the grains of that genus. There is, however, not much likelihood of confusing the grains of the two genera even if the bands do not show, because the majority of *Alnus* grains are four-pored, while the majority of *Pterocarya* are five- or six-pored.

The grains of *Engelhardtia spicata* are almost the same as those of some of the Betulaceae, especially *Corylus*. In fact there is great danger of confusing them. They are, however, about 19–22 μ in diameter, which is somewhat smaller than those of *Corylus* or other Betulaceae.

The grains of *Platycarya* are similar in form to those of *Engelhardtia*,

but are smaller, measuring only 14μ in diameter and their apertures are narrow and almost slit-like. A further discussion of the grains of this family in comparison with those of the Betulaceae will be found under that family.

Hicoria

In the oil shales are a large number of pollen grains which are undoubtedly those of *Hicoria*; they differ from living species only in their size. The two fossil species which I have distinguished range from 31.2 to 39μ in diameter, while the grains of the living species which I have examined ranged from 42 to 52μ in diameter. The fossil grains were apparently lens-shaped in life, though the specimens are greatly flattened dorsiventrally. They have three pores confined to the ventral surface, and their exine is smooth or slightly granular particularly around the pores.

The hickories are represented in the Green River flora by a single known species, *H. juglandiformis* (Sternby) Knowlton, a species which also occurs in the Miocene Latah and Florissant formations, and was apparently wide-spread and abundant in Tertiary times. It is therefore quite possible that one or the other of the two following fossil grains belongs to that species, though by no means certain, for in Tertiary times the genus was represented by a number of other species. For example there are recorded two in the Jackson Flora, one in the Claiborne (6), and Wilcox (10) and two in the Tertiary of British Columbia (8). Any or all of these might have been present in the Green River flora, though not yet recorded. Furthermore it is quite possible that the two fossil grains described below represent more than two natural species, for the forms of the various living hickories are not usually distinguishable from each other.

***Hicoria viridi-fluminipites* sp. nov.** (fig. 29). Oblately flattened and rounded triangular in outline, 36 – 39μ in diameter; pores 3, near the equator of the grain, circular or slightly elliptical with their long axes directed meridionally, 2.3 – 3.4μ long. *Holotype*: 5 – 17.5 – 45.0 .

This grain is unquestionably that of a species of *Hicoria*. It matches in all respects, except its smaller size, that of *H. Myristicaeformis*. Therefore it probably represents a species which does not exist at the present time but was related to the *Myristicaeformis* group of hickories. It occurs in the oil shales in great abundance and many of the grains are perfectly preserved. Its specific name refers to the fact that it is a characteristic form of the Green River shales.

From the Miocene brown coals of Europe a similar form of grain is described as *Pollenites globiformis* by Potonié (41), which may be the same species.

Hicoria juxtaporipites sp. nov. (fig. 30). Similar to the preceding, 31.2μ in diameter; pores circular, 2.3μ in diameter, not close to the equator, closer to each other and arranged in a triangle. Exine fine granular. *Holotype*: 5-13.1-41.9.

A single grain of this species was found. It is less like any present day species than is the preceding, but is included here because it undoubtedly belongs to the family and is more like the grains of *Hicoria* than those of any other existing genus.

Juglans nigripites sp. nov. (fig. 31). Grain apparently lens-shaped in life, though the fossil is greatly flattened dorsiventrally in the plane of the section, 40μ in diameter. Visible pores eleven, short elliptical, about 2.2μ long, eight of them are on or nearly on the equator and three on the ventral (lower) surface, but none on the dorsal. Exine rather thick and slightly thicker around the pores, texture finely and faintly granular. *Holotype*: 5-17.2-45.4.

A single specimen of this species was found. It is in a perfect state of preservation and, owing to its transparency both sides are visible. It may, however, have twelve instead of eleven pores. It belongs unquestionably to *Juglans*. It cannot, however, be matched exactly with any living species of which pollen is available. In size it compares favorably with *J. regia* 41.6μ in diameter, but the pores of the latter are circular and larger, 3.3μ in diameter, and fewer in number, 6-11, generally fewer than eleven. On the other hand the pores of the fossil are more numerous than those of *J. cinerea* (5-8). The fossil matches the grains of *J. major*, *J. californica* and *J. nigra* about equally well, though it is too small for any one of these; their sizes are about 34.2 , 36.5 and 34μ in diameter, respectively.

Juglans is represented by five known species in the Green River flora, but it is, at present impossible to state to which, if any of these, this fossil grain belongs. *Juglans* is an ancient group, with a history dating back to the Upper Cretaceous (3). In the Tertiary it was represented by many different species and is a conspicuous feature of most of the Tertiary floras, particularly those of the more northerly and colder climates, as for example the Siberian (33), Sakhalin Island (32), and Greenland floras; and in America it occurs in the Denver (31), Wilcox (10) and Raton (36). In the warmer floras it is represented by only a single species in the Claiborne and is absent from the Jackson.

Engelhardtia corylipites sp. nov. (fig. 32). Oblately flattened, triangular in outline, 21.1 - 23μ in diameter; pores three at the angles, pore diagram as in *Corylus* (fig. 38), with the rim slightly roughened inside. Exine smooth. *Holotype*: 3-12.0-44.0.

Only two specimens of this species were found. They match exactly the grains of *Engelhardtia*, except for a slight difference in size (those of *Engelhardtia spicata* range from 19.4–21.6 μ) which is not significant. Nevertheless it is with some hesitation that these fossils are assigned to this genus, because it is only their small size which distinguishes them from the grains of the species of *Momisia* and *Corylus* which I have examined, so they may match as closely some species of these or even other genera that I have not

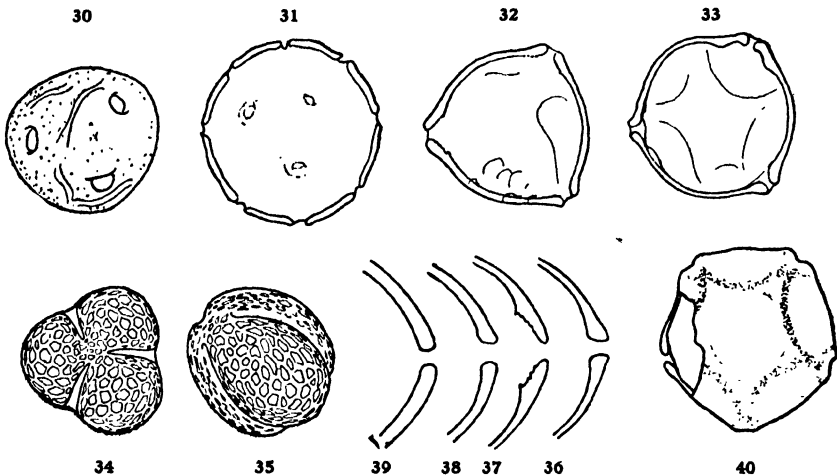


Fig. 30, *Hicoria juxtaaporipites*, ventral view; fig. 31, *Juglans nigripites*, optical section. Three pores occurring on the ventral surface, which can be seen through the grain, are dotted; fig. 32, *Engelhardtia corylipites*, optical section; fig. 33, *Myricipites dubius* optical section; figs. 34, 35, *Salix discoloripites*, fig. 34, polar view, fig. 35, side view; figs. 36–39 pore patterns as seen in optical section, of some aspidate grains; fig. 36, “broad-knob” or *Betula* pattern; fig. 37, the *Tarsus* or *Myrica* pattern; fig. 38, the club-shaped or *Corylus* pattern; fig. 39, the “unexpanded” or *Carpinus* pattern; fig. 40, *Alnus speciiipites*, drawn as if a part were removed, to show its appearance in optical section.

yet seen. Their specific name refers to the resemblance that these grains bear to those of *Corylus*.

Engelhardtia has not previously been recorded from the Green River formation, but it is to be expected there because it is represented in the Florissant of Colorado (18), which is regarded as a Miocene derivative of the Green River flora. It has also been recorded from the Eocene Wilcox (10) and Jackson (6) floras.

MYRICACEAE

Myricipites gen. nov.

Approximately spheroidal. Pores three, greatly protruding, of the tarsus pattern (fig. 37). Texture smooth.

Myricipites dubius sp. nov. (fig. 33). Grains 25.1μ in diameter. Texture of the present specimen wrinkled but probably smooth in life. *Holotype*: 25/8-13.2-49.4.

Only a single specimen of this species was found and it is badly shrunken and wrinkled. My reason for assigning it to *Myrica* is based principally upon the character of the thickenings surrounding the pores. In the present specimen, however, this appearance may be due to its shrunken condition.

About eight species of *Myrica* have already been distinguished in the Green River formation. It is one of the most abundant and widely distributed genera of the Tertiary, occurring in practically all of the floras of that epoch. It was also present in the Upper Cretaceous period (3) and is still widely distributed though greatly reduced in number of species.

SALICACEAE

Salix discoloripites sp. nov. (figs. 34, 35). Tricolpate and generally more or less deeply three lobed, isodiametric, slightly elongate or oblately flattened, according to the degree of expansion; $13.7-23.9\mu$ in diameter. Furrows long and tapering, without internal marginal thickenings and without germ pores. Exine thick and coarsely reticulate, with the network generally finer towards the margins of the furrows and towards the poles. *Holotype*: 5-14.25-44.9.

These grains match exactly those of the two living species, *S. discolor* and *S. fragilis*, with which I have compared them, and I know of no other grains, other than those of willow, with which they could be compared,—their lack of germ pore and furrow thickenings seems to be distinctive. These grains are extremely numerous, possibly the most abundant of any species in the shales. In view of the fact that the willows are primarily insect pollinated and are not profuse pollen shedders, the large numbers of their grains found in the shales attest to the enormous abundance of the willows in the Green River epoch and their proximity to the place of deposition. The suggestion naturally occurs that possibly these grains belong to some species closely related to *Salix* but which is wind pollinated, for example *Populus*. In this connection, therefore it should be pointed out that the pollen grains of *Populus* bear no resemblance to those of *Salix* and could not possibly be confused with them. No grains of *Populus* were found in the oil shales though the trees are enormously productive of pollen and are believed to have flourished abundantly during the Green River epoch. The grains of *Populus* are provided with only a thin, almost fragmentary, exine, and I suspect that their absence from the Green River shales is attributable to their fragile nature.

Four species of *Salix* have been recorded from the Green River formation (17, 27) and one from the Wind River Basin of Wyoming of Green

River age (11); willows are also common in other floras of Tertiary age. What appears to be the pollen of the same species as the present one is described by Potonié (40) as *Pollenites fraudulentus* Pot. from Eocene brown coal of Germany.

BETULACEAE

The grains of the living Betulaceae are smooth or only faintly granular, spheroidal or more or less oblatelly flattened, 20–35 μ in diameter, provided with three to seven germ pores which tend to be equally spaced around the equator. In shape the germinal-apertures differ in the different species, being circular, elliptical or slit shaped. When the apertures are elongate they are meridionally oriented, or with their major axes converging in pairs, if there are more than three. The most distinctive character of these grains, however, is that their germ pores always protrude as rounded domes, and give the grains when seen in polar view an angular outline. This character I have called 'aspidate' owing to the resemblance of such a protruding pore to a small circular shield or *aspis*. The dome-shaped protrusions are due to a thickening of the intine underlying the region immediately surrounding the pore, and frequently also to a lesser annular thickening of the exine.

All of these characters the grains of the Betulaceae share with those of the Myricaceae, *Myriophyllum* among the Haloragidaceae, *Platycaria*, *Engelhardtia* and *Pterocarya* among the Juglandaceae, and *Momisia* among the Ulmaceae; and they closely resemble the grains of *Broussonetia*, *Morus*, *Humulus* and *Cannabis* among the Urticaceae. In fact they represent a form towards which the grains of many wind-pollinated species of diverse origins tend to approach. This, together with a close intrafamily resemblance of the various genera makes the recognition of the pollen grains of the Betulaceae always difficult and occasionally uncertain.

They can generally be distinguished, however, by certain minor characters which they possess individually. One such character is found in the annular thickening of the exine surrounding the pore. When seen in optical section with the pore at the plane of focus, the germinal aperture appears as a gap at which the walls on either side end with knob-like thickenings, which vary in the different species.

Passing in review the grains of the members of the Betulaceae and those of families with which it is possible to confuse them, four fairly well marked types of pore pattern may be distinguished. These are (1) the broad-knob or *Betula* pore pattern (fig. 36) in which the exine appears in optical section to end at the pore in a broad and abrupt expansion, and the pores, as a consequence of the thickening of the exine, are raised sharply above the

surface of the grain. This pore pattern is characteristic of all species of *Betula*, *Myriophyllum* and, with a slight modification towards the next type, of *Alnus*. (2) the tarsus or *Myrica* pore pattern in which the wall thickness suggests in appearance the shape of the terminal joint or tarsus of the hind legs of some insects (fig. 37). This form in its fullest development characterizes the grains of *Myrica* and *Comptonia*, and is somewhat approached in those of *Engelhardtia* and *Alnus* (3), the club-shaped or *Corylus* pore pattern (fig. 38) in which the exine is only slightly and gradually expanded at the pores; consequently in such grains the pores are only slightly raised above the surface. This form characterizes the grains of *Corylus*, *Pterocarya*, *Platycarya* and *Momisia*, and, with a certain tendency towards the tarsus pattern, those of *Ostrya* (4), the unexpanded or *Carpinus* pore pattern (fig. 39). In this the walls of the exine are not at all or only very slightly expanded at the pores. It must be admitted the distinction between this and the previous pore pattern is often vague. This pattern characterizes the grain of *Carpinus* and, with a modification towards the tarsus type, that of *Engelhardtia*. Fortunately we are further aided in the identification of these two grains by the fact that that of *Carpinus* is the largest while that of *Engelhardtia* is the smallest of all of the grains possessing this pore pattern.

Alnus speciipites sp. nov. (fig. 40). Lens-shaped. 20–30.4 μ in diameter; pores 4 or 5, occasionally 3 or 6, arranged around the equator with the long axes of their apertures which are elliptical converging in pairs. Exine smooth or slightly roughened, greatly thickened in the region immediately surrounding the pores causing them to protrude markedly (fig. 36) and giving the grain an angular appearance. The exine is also thickened along linear bands following geodetic curves between the pores. *Holotype*: 3–11.9–41.6.

These grains are common in the oil shales, and are among the most conspicuous elements found, hence their specific name. They conform in all respects to those of living species of *Alnus*. In size they show a greater range of variation than I have encountered in the pollen of a single living species, consequently it is likely that more than one natural species is involved, but they are well within the size limits of the genus.

The presence of the connecting bands, when these are in evidence, makes the recognition of these grains easy and their identification with the genus *Alnus* certain. Similar bands, it is true, occur in the grains of *Planera*, but these grains are entirely different in other respects. Without the bands the grains of *Alnus* could scarcely be distinguished from those of some species of *Myriophyllum*, *Pterocarya*, and of *Carpinus Betula*; consequently grains of *Alnus* in which the bands are not in evidence, as is

sometimes the case, might confuse the identification of these latter species in any but perfectly preserved specimens.

Alnus pollen grains with both 4 and 5 pores, apparently identical in all respects with those described above have been reported by Kirchheimer (24, 25) from European brown coals. Also grains with 4–6 pores have been reported by the same author but these are of a considerably smaller size and are, therefore, of a different species but the connecting bands between the pores are quite distinct, Kirchheimer points out that, though these grains are smaller than any of *Alnus* with which he has compared them, they are found in association with numerous fossil leaves and flowers which have been identified as *Alnus gracilis* Ung., *A. Kefersteini* Göpp., *A. nostratum* Ung., which is strong evidence that they are truly alder grains. Moreover these small grains of Kirchheimer's appear to be the same as *Alni-pollenites verus* Pot. described by Potonié (41) from Miocene brown coal of Germany. Potonié (38) also describes, under the name of *Pollenites coryphaeus tetraexitum*, grains from Miocene brown coal which correspond to the present species but do not show the connecting bands.

No species of alder have yet been described from the Green River formation but the alders have left their records in most of the larger Tertiary deposits. They occur in the cold Siberian Tertiary (33). In the Tertiary of B. C. they are represented by three species (8). In the Florissant they are represented by two species (26). In the Miocene Latah formation (9) they are represented by two species, including a staminate-catkin and a pistillate cone (29), and in the Denver by two species (31). So it is not surprising that alder pollen is found in the Green River shales and one can predict with certainty that other parts of the plant will be found as the shales are more extensively studied.

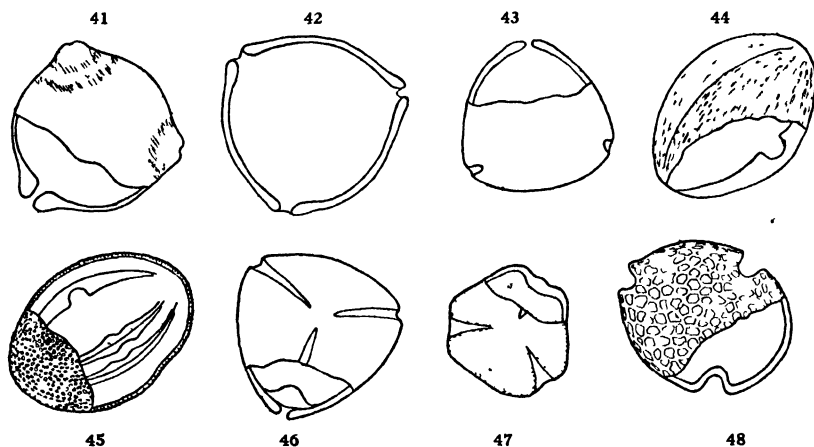
***Betula claripites* sp. nov.** (fig. 41). Apparently spheroidal or oblatelately flattened in life. 22.8–29.6 μ in diameter; pores three, protruding owing to the thickening of the exine surrounding them, pore pattern corresponding to the *Betula* type (fig. 36), apertures approximately circular; aspidies faintly visible; texture smooth. *Holotype*: 4–8.8–65.1.

These grains match perfectly those of living species of *Betula*, coming perhaps closest to *B. lenta*, and are not likely to be confused with any other member of the family. Only two grains were found which certainly belong to this species and a third, imperfectly preserved, which probably does. Their rounded shape and sharply protruding pores make them rather conspicuous objects, and it is to this fact that the specific name refers, but they are much less abundant than the pollen of *Carpinus* or *Alnus*.

The leaf of a single species of birch (*Betula eocenica* R. W. Brn.) has

been recorded from the Green River formation (17), but, unless a staminate cone bearing recognizable grains is found, it is unsafe to assume that the pollen is of the same species. Similar grains but somewhat smaller, so undoubtedly of another species, have been described from Tertiary brown coals (24).

Betula has a wide distribution in Tertiary formations. It is found in the cold Siberian Tertiary (33), and in most of the principal Tertiary floras of America except those of the southeast regions which were too warm (6).



• Fig. 41, *Betula claripites*, polar view, drawn as if a part were removed, to show its appearance in optical section; fig. 42, *Carpinus ancipites*, optical section, polar view; fig. 43, *Momipites coryloides*, polar view drawn as if a part were removed, to show its appearance in optical section; fig. 44, *Ailanthipites Berryi*. Side view, drawn as if a part were cut away, to show the inwardly projecting rims of the furrow and germ pore; fig. 45, *Rhoipites Bradleyi*, side view, in optical section except a small part at the upper end which is shown in surface view; fig. 46, *Talisiipites Fischeri*, polar view showing a small part of one side in optical section; fig. 47, *Vitipites dubius*, polar view of surface, a small part on one side shown in optical section; fig. 48, *Tilia crassipites*, polar view of surface on the left and optical section on right.

It is represented in the Florissant (26), in the Latah Miocene (9, 29), in the tertiary of B. C. (8), and in the Denver and associated formations (27). The presence of *Betula* and *Alnus* in the Green River flora suggest a rather cool and humid climate.

***Carpinus ancipites* sp. nov.** (fig. 42). In life apparently oblately flattened angular in outline, 27.4–44.5 μ in diameter. Pores 3 or 4, their apertures elliptical; when three, meridionally arranged; when four, on the equator with their major axes converging in pairs; very slightly or not at all protruding, and the exine surrounding them scarcely or not at all thickened, pore pattern as in the *Carpinus* type (fig. 39). Texture smooth. *Holotype*: 4–19.1–72.1.

These grains match exactly the two species of *Carpinus* which I have examined, but in size they have a greater range of variation. They are rather numerous in the shales, but much less so than *Momipites* which they resemble closely. The specific name is derived from Lat. *anceps*, ambiguous, on account of the difficulty of distinguishing them from this latter species.

Carpinus has not hitherto been recorded from the Green River formation, though it was much more abundant, both in species and individuals, during Tertiary times than it is at present, and it is represented in most of the principal Tertiary floras of America except those of the southwest of which the climate was too warm for the Betulaceae.

ULMACEAE

Momipites gen. nov.

Grains spheroidal or oblatelly flattened and somewhat triangular in outline. Pores three on the equator with their apertures broadly elliptical and meridionally oriented, only slightly protruding above the surface, and with the exine immediately surrounding them slightly thickened, corresponding to the *Corylus* pattern (fig. 38). Texture smooth.

Momipites coryloides sp. nov. (fig. 43). Oblately flattened and triangular in outline, 21–33.1 μ in diameter. *Holotype*: 5–10.9–52.7.

These grains are numerous in the oil shales and many of them are so perfectly preserved that the outlines of the subexineous thickenings which surrounded their germ pores in life can be clearly seen. Nevertheless their identification with *Momisia* is not entirely certain for they are scarcely distinguishable from the grains of *Corylus*. They likewise match *Engelhardtia spicata* in all respects except their larger size. But by actual comparison they seem to match most closely the grains of *Momisia*, especially *M. iguanacea*, accordingly they are tentatively referred to this genus.

Neither *Momisia*, *Engelhardtia*, nor *Corylus* have been recorded from the Green River formation, but all three are common genera of North American Tertiary deposits. *Engelhardtia* occurs in the Jackson, Wilcox and Florissant floras, which latter is in part probably a Miocene derivative of the Eocene Green River flora. *Corylus* is known to occur in the Tertiary of British Columbia (8). *Momisia* occurs in the Clairborne and Jackson floras (6). Though *Momisia* has not been recorded as such from the Green River formation, *Celtis debequensis* R. W. Brn. has, and since *Momisia* is regarded by many botanists as a section of the genus *Celtis*, I feel that there is at least a possibility that the pollen, here designated as *Momipites coryloides*, may be that of *Celtis debequensis*.

It is unfortunate that the identification of this pollen cannot be determined with greater certainty because, occurring in the enormous quantity

that it does in the oil shales, it must have come from one of the dominant members of the Green River flora. If it turns out to belong to *Momisia* or *Engelhardtia* it points to southern connections of the Green River flora, but if it turns out to belong to *Corylus* it points to the northern connection of this flora.

Similar pollen grains are described from Eocene brown coal of Germany by Kirchheimer (24). He suggests that such a form might belong to some member of the Betulaceae, especially *Corylus*, but, he states, it is also closely approached by the grains of *Ostrya* and *Myrica*. I do not feel that there is any danger of confusing the present species from the Green River formation with either of these two latter genera.

SIMARUBACEAE

Ailanthipites gen. nov.

Generally ellipsoidal, but somewhat various in shape according to the degree of their expansion, tricolpate with furrows long, reaching almost from pole to pole, furrow rim and pore rim conspicuous, projecting deeply inward. Exine reticulate-pitted with the pits elongate and linearly arranged forming a sort of thumb-print pattern.

Ailanthipites Berryi sp. nov. (fig. 44). Grains $20-25.1\mu$ broad and $26-30\mu$ long. *Holotype*: 36-19.8-61.5.

These grains match perfectly those of *Ailanthus glandulosa*, and it is with a fair degree of confidence that they are assigned to that genus. The only other form of grain I know which they resemble is that of *Spondias Mombin* (46), but the grains of the latter are much larger— $34-39\mu$ broad and $43-50\mu$ long—which makes it extremely unlikely that these fossils belong to that genus. They are obviously insect borne yet they occur in the shales in large numbers. Therefore, they belong to a plant which grew abundantly near the place of deposition.

Ailanthus is represented in the Green River flora by the fossil species *A. longi-petiolata* Lesquereux. There is, therefore, at least a possibility that these grains belong to that species. "The Chinese tree of heaven (*Ailanthus*) is found fossil in the late Miocene lake beds at Florissant, Colorado and at other places and times in North America, but has not been native for hundreds of thousands of years, yet it has become effectively naturalized in the last few centuries since it was introduced by man." The specific name is given in honor of Edward W. Berry from whose work the quotation is taken, and who has contributed perhaps more than any other single investigator to our knowledge of Tertiary floras.

ANACARDIACEAE

Rhoipites gen. nov.

Ellipsoidal, tricolpate, with furrows long and pointed. Furrow and pore thickenings conspicuous, projecting deeply inwards. Exine rather finely reticulate-pitted.

Rhoipites Bradleyi sp. nov. (fig. 45). Grains $25 \times 35 \mu$. *Holotype*: 36-19.6-61.8. *At this reading are four grains of this species. The holotype is the one illustrated.*

This species matches perfectly with the grain of *Rhus typhina*. It is, however, of a generalized type which makes the evidence of matching alone, somewhat uncertain. It is rather abundant in the shales, and since it has the appearance of being primarily insect pollinated the plant which produced it must have lived in great abundance and close to the place of deposition.

Rhus is represented in the Green River flora by five species, and from the same family have been recorded one species of *Schmaltzia* and one of *Anacardites*. *Rhus* is also known from the Raton (36), Animas (28) and Latah (9, 29) formations. Consequently the finding of *Rhus* pollen in the Green River oil shales is to be expected. The specific name of the present species is given in honor of W. H. Bradley in recognition of his studies of the Green River formation.

SAPINDACEAE

Talisiipites gen. nov.

Oblately flattened, triangular in polar view, tricolpate, with furrows long, narrow and shallow, each enclosing a small germ pore. Pores aspidate, surrounded by a subexineous thickening similar to those of the grains of the Betulaceae. Exine thin and rather finely granular, more evidently so near the pores.

Talisiipites Fischeri sp. nov. (fig. 46). Grains 28.5μ in diameter. *Holotype*: 3-10-44.5.

These grains are rather common, four were examined in detail. They match perfectly *Talisia depressa* (46). Since this is rather a unique type in its combination of aspidate pores with long tapering furrows, one that I have not encountered elsewhere, it is with a fair degree of confidence that it is assigned to the genus *Talisia*. The specific name of these grains is given in honor of Hugo Fischer whose inaugural dissertation, dated Breslau 1890, has become a classic in pollen literature.

A species of this family, *Thouinia* (*Talisia*) *eocenica* R. W. Brn., is

represented in the Green River formation and it is indeed possible that the grains described here belong to that species. What appears to be the same species is described by Potonié (40) as *Pollenites vestibulum* from Eocene brown coal of Germany.

VITACEAE

Vitipites gen. nov.

Oblately flattened, hexagonal in polar view, rather small, tricolpate with furrows sharply defined, long and tapering. Exine finely and faintly pitted.

Vitipites dubius sp. nov. (fig. 47). Grains about 22.8μ broad. *Holotype*: 4-8.5-66.3.

A single specimen of this species was found. It matches exactly with the pollen grain of *Vitis vinifera*. Nevertheless since it is of a rather generalized type its identification with the genus *Vitis* is not entirely certain.

Vitis has not hitherto been recorded from the Green River formation, but is known to occur in its derivative flora, the Miocene Florissant. It has also been recorded from the Denver, Vermejo and Raton formations (31) so it is to be expected in that of the Green River. An allied species, *Parthenocissus tertiaria* (Lesquereux) Knowlton has been recorded from this formation (27), but the pollen grains of the living species of these two genera are quite distinct and not likely to be confused.

TILIACEAE

Tilia

Grains of the living species, *T. americana*, are lens-shaped, $35.3\text{--}37.6\mu$ in diameter, always with three germ pores arranged around the equator and deeply sunken in very short pit-like germinal furrows, with exine rather thick and finely reticulate-pitted.

Among the present fossil material are found four distinct forms which answer more or less closely to this description.

The other members of the Tiliaceae, *Triumfetta* and *Grewia*, which are believed to have been widely represented in Eocene time, have pollen grains entirely different. Those of both *Triumfetta* and *Grewia* are ellipsoidal, $43\text{--}54\mu$ long and about $2/3$ as broad, with long tapering furrows reaching almost from pole to pole, and with coarsely reticulate exine. I did not find them represented in the oil shales, nor is there any possibility that any of the fossil material here included under *Tilia* can belong to either of these genera.

Tilia has not hitherto been recorded from the Green River formation, and the family is, up to the present, represented in that formation only by

a single species of *Grewiopsis*. But *Tilia* was rather wide spread in the Tertiary period. It is recorded from the Eocene Jackson and Raton floras (36) and from the Miocene Latah (9) and Florissant (18, 26) floras, so it is to be expected in that of the Green River.

Two species of *Tilia* pollen, *Tiliae-pollenites instructus* Pot., and *T.-p. indubitabilis* Pot. which may be the same as *T. crassipites* among the following, have been described from the European brown coals by Potonié (39), but he states that they are granular whereas the following are reticu-

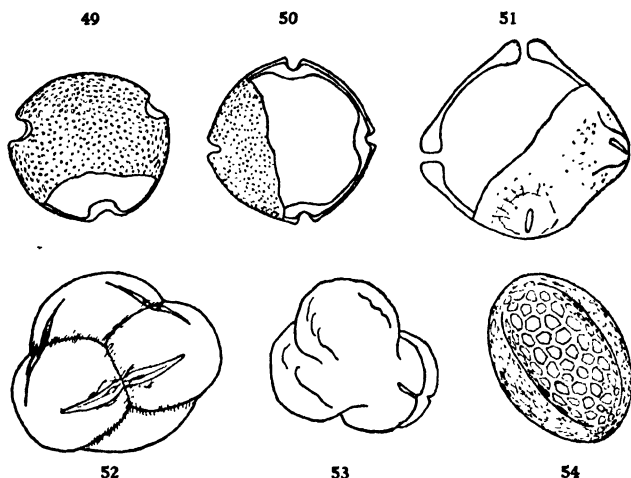


Fig. 49, *Tilia vescipites*, polar view of surface, but with a small part shown in optical section; fig. 50, *Tilia tetraforaminipites*, polar view, the left of the figure in optical section, the right in surface view; fig. 51, *Myriophyllum ambiguipites*, polar view shown partly in optical section and partly in surface view; fig. 52, *Ericipites longisulcatus*, a tetrad of united grains; fig. 53, *Ericipites brevisulcatus*, a tetrad of united grains; fig. 54, *Caprifoliipites viridi-fluminis*, side view.

late-pitted as are those of the living *T. americana*. Kirchheimer (24), also describes and illustrates a species of *Tilia* pollen from the Tertiary brown coal of Germany, but it is apparently not the same as any of those described below for it is $31.2\text{--}40.3\mu$ in diameter and is stated to be granular.

***Tilia crassipites* sp. nov.** (fig. 48). Grains apparently lens-shaped or at least somewhat oblately flattened in life, though the present specimen is completely flattened in the plane of the section and somewhat distorted, $43.3 \times 36.5\mu$. Pores three, sunken in deep pits. Exine thick and coarsely reticulate. *Holotype*: 4-8.6-65.2.

This fossil bears a marked resemblance to the grain of *Tilia americana* but differs in its larger size and more coarsely reticulate surface. It is to this character that the specific name refers.

Tilia vespipites sp. nov. (fig. 49). Similar to the preceding, but 27.4μ in diameter and with exine finely reticulate-pitted. It is to the fineness of the texture that the specific name refers. *Holotype*: 5-10.8-48.9.

This fossil matches exactly the grain of *T. americana* except for its size which is about 10μ in diameter less.

Tilia tetraforaminipites sp. nov. (fig. 50). Similar to the preceding, except that the exine is more finely pitted, and there are four instead of three pores, 28.5μ in diameter. *Holotype*: 6-16.1-62.4.

Three specimens of this species were found but only one is well enough preserved to permit its recognition with certainty. This species matches almost exactly the grain of *Tilia americana*, except in its possession of four pores. Though the pollen of the living *Tilia americana* appears to be always three pored, that is no reason why other species should not have four pores in all or some of their grains, because the number of germ pores possessed by a pollen grain, whether three, four, six or even higher numbers, may be a specific, generic or family character, or merely a matter of individual variation.

HALORAGIDACEAE

Myriophyllum ambiguipites sp. nov. (fig. 51). Oblately flattened and decidedly angular in outline 21.6μ in diameter. Pores four, abruptly protruding above the surface of the grain and surrounded by a greatly thickened ring of the exine, of the *Betula* pore pattern (fig. 36) with apertures slit-shaped and converging in pairs. Exine slightly granular, particularly around the pores. *Holotype*: 3-11.9-41.0.

Only a single specimen of this species was found. It matches exactly with the grains of *Myriophyllum spicatum* L. and I believe that the rather extreme and abrupt thickening of the exine surrounding the pores is distinctive. To some extent this fossil species resembles the grain of *Alnus*, but lacks the connecting bands of the latter. It also resembles the four-pored grains of *Comptonia*, but the germinal apertures of these are never slit-shaped, being instead, circular or broadly elliptical.

Myriophyllum has not been recorded from the Green River formation, nor, so far as I am aware, elsewhere in the Tertiary.

***Ericipites* gen. nov.**

Grains in tetrahedral tetrads, generally tightly appressed. Exine rather thin, smooth or somewhat granular. Furrows of each grain of the tetrad three, of various length in the different species; each contiguous and continuous with one of the furrows of each of its three neighbors across the suture between

their contact faces. Pores three, enclosed by the furrows, those of adjacent furrows close to and facing each other across the suture.

Among the living species of Ericaceae the pollen grains of the majority answer this description. But those of the Clethraceae and Monotropaceae which are frequently, though probably mistakenly, included in the family, are always single. Among the true Ericaceae the grains of many species, as for example those of *Rhododendron*, *Kalmia* and some species of *Erica* are provided with extremely slender 'vicin' threads which cause them to become tangled together in large numbers as they leave their anthers. There is much of a sameness of pollen form throughout most of the family, but such characters as the size of the grains, the length and breadth of the furrows, and the texture of the exine can sometimes be used to distinguish the different genera from each other. Even among living species, however, these distinctions are vague and difficult of interpretation, consequently the present fossil genus is established to receive all fossil pollen which is known to belong to the family Ericaceae, exclusive of the Clethraceae and Monotropaceae, which are in reality almost unrelated to the true Ericaceae.

A single species of Ericaceae, *Andromeda delicatula* Lesquereux has been previously recorded from the Green River formation (27), and the genus is also found represented in the Florissant beds (18) and Raton formation (36), but neither of the two fossil species recorded here match the grains of living species of *Andromeda*. Pollen of several kinds of Ericaceae are recorded from Tertiary brown coals of Europe (24, 41).

Ericipites longisulcatus sp. nov. (fig. 52). Tetrads 36–45.6 μ broad. Exine mostly smooth but faintly roughened in some regions. Furrows long and slender, tapering to their distal ends; the presence of pores enclosed by each is indicated by a slight bulge near its proximal end. *Holotype*: 4-19.8-70.1.

Only two specimens of this species were found, and they are in actual contact with each other. The faintly granular appearance of some parts of the exine suggests that in life these grains were granular throughout, as are those of most living Ericaceae. No vicin threads were observed, but the fact that the only two specimens that were found are in contact with each other is strong evidence that they arrived at their place of entombment tangled together by such threads. In the grains of *Andromeda*, the only member of the Ericaceae so far recorded from the Green River formation, such threads are lacking; furthermore the furrows of the grains of *Andromeda* are much broader and shorter than those of the present fossil species, consequently it cannot be *Andromeda*. In this and other characters

the present fossil species resembles more closely the grains of some species of *Erica*.

Ericipites brevisulcatus sp. nov. (fig. 53). Tetrads 45.6μ broad. Exine smooth. Furrows short. *Holotype*: 8-5.5-62.8.

A single specimen of this species was found, and it is in so poor a state of preservation that no details further than its general resemblance to the Ericaceae could be seen. As far as these observations go it corresponds with *Calluna vulgaris* Salisb.

CAPRIFOLIACEAE

Caprifoliipites gen. nov.

Grains very small, among the smallest found in the oil shales, ellipsoidal, tricolpate with furrows long and pointed, with conspicuous internally projecting furrow rims and pore rims. Exine coarsely reticulate.

Caprifoliipites viridi-fluminis sp. nov. (fig. 54). Grains 11.4 – 17.1μ broad and 16.5 – 22.8μ long. *Holotype*: 36-7.3-60.7.

These beautiful little grains are among the most abundant species in the shales, and since they are nearly always perfectly preserved they form one of the most conspicuous and characteristic elements of the shales, hence their specific name. In form they match almost perfectly with the grains of *Viburnum*, but in their small size they compare more favorably with the very similar grains of *Sambucus*. Unfortunately, however, these fossil grains represent a generalized type, so that their assignment to the Caprifoliaceae is little more than a guess, though I believe it has a fair degree of probability.

The Caprifoliaceae are not represented in the Green River flora but are found in the Miocene Florissant of Colorado. *Viburnum* was an exceedingly widespread and characteristic genus of Tertiary times occurring in the Vermejo, Raton, Denver, Animas, Wilcox and Latah formations, so it is to be expected in the Green River flora.

SUMMARY AND CONCLUSIONS

From the oil shales of the Eocene Green River have been described forty-three species of fossil pollen, in thirty-four genera. All, except one, are assignable to living genera or families. One species is an abietineous grain belonging to an extinct genus. There still remain in the material examined possibly twice as many more pollen species awaiting identification.

The list of families and genera of plants that have been found to be represented in this material by pollen is shown in Table I. Of these, twenty-

nine species (21 genera) are new to the Green River flora, while only eighteen species, in thirteen genera, are of genera already represented in the Green River flora. This disagreement between the fossil pollen record and the fossil record of other parts of plants, is apparently due, in part at least, to the greater mobility of pollen. Twenty-nine of the pollen species were probably wind borne, and most of these are of plants which do not grow in or near water, so had little chance, except through their pollen, of ever being represented in the oil shales, which were laid down in water. A further study of the unidentified pollen in the material is likely to only increase this disagreement, because the examination of the material was prefaced by a study of the pollen of the living representatives of the Green River flora, making their recognition fairly certain if encountered.

On the whole the flora, as indicated by the pollen record, was decidedly less tropical in nature than that already recorded from the Green River formation. This appears to have been due to the fact that the two records are not entirely contemporaneous. In a private communication upon this subject Dr. Bradley states, "On the basis of the varves or annual layers in certain beds of the Green River formation, I have estimated that the leaf-bearing horizons were deposited at least one million years later than most of the pollen-bearing oil shales which you have been studying. The basis for estimating this time interval is given in another paper of mine, Professional Paper 158, in which I also discuss some aspects of the Green River climate. According to this estimate the time interval between the pollen beds and the greater part of the known Green River flora is amply long for a rather distinct climatic change. In as much as some of the lowermost beds in the Green River formation also contain a flora which is nearly if not quite identical with that obtained from the uppermost beds, it seems that the oil shale was formed during low stages of the lake under considerably drier conditions than those prevailing either during the lower part of the Green River epoch or during the latest phases of it. This idea is further strengthened by the fact that salt crystal molds are commonly associated with the oil shale beds."

That the pollen beds were deposited during a period of extreme aridity is confirmed by the finding of the pollen of *Ephedra* which is a desert plant. Nevertheless the bulk of the pollen at exactly the same level was contributed by trees of a forest type similar to that of the northern and middle Atlantic states of the present time, demanding conditions entirely different from those congenial to *Ephedra*.

With such evidences at hand one can hardly refrain from hazarding a reconstruction of the ancient Green River lake and the conditions surrounding it. The lake must have lain in a hot desert valley, and have

been fed by streams flowing into it from regions where there was heavier rainfall. The lake was shallow and muddy, possibly consisting of a succession of small ponds, as suggested by Brown (17), for in the water grew pondweeds (*Potamogeton*), water milfoils (*Myriophyllum*), and along its margins arrow arum (*Pellandra*). Immediately surrounding the lake must have been extensive marshy areas in which grew cypress (*Taxodium*), the water pine (*Glyptostrobus*), some heaths, and quantities of willows (*Salix*), and in less marshy regions a few palms and cycads amid the usual underbrush, including such shrubs as the marsh elders or possibly viburnums, and sumacs, and the usual tangle of vines as the wild grapes (*Vitis*) and cat-briars (*Smilax*). Here also grew *Myrica*. Its pollen is of such a character that it could have been carried from the hills several miles away, but the presence of eight species already recorded by abundant material of leaves and stems in the shales, suggests that the pollen came from species which grew in or near the water.

All of these and the numerous other plants whose substance went to make up the beds must have derived their moisture from the lake itself, for the presence of *Ephedra* pollen in the shales indicates that the region was surrounded by arid conditions not very far away, just as certainly as the presence of salt crystal molds indicates that from time to time the lake partly dried up. But the mountains surrounding the lake must have been well watered, a condition which prevails in much of the arid regions of the southwestern part of the United States today. At the higher altitudes flourished a mesophytic forest, dominated by pines, firs, spruces, with a sprinkling of hemlock, possibly *Cedrus* and one or more species of conifer unknown to us. That this rich coniferous forest flourished a long way from the lake is attested by the fact that it has hitherto only been represented in the lacustrine deposits by a single winged seed and a small twig. Intermingled with these, but in considerably lesser numbers, were hickories, walnuts and *Engelhardtia*, with birches and basswood barely able to maintain a foothold, and here and there a tulip tree or magnolia. Leading down from these well watered mountains were small canyons in which grew thickets of alder and ironwood (*Carpinus*). That these did not grow near the lake itself is suggested by the absence, so far discovered, of their leaves etc. in the shales.

Something should be said of the pollen which was not found, though, of course, anything said on this score may be contradicted by further studies. Herbaceous plants, apart from a few aquatics are not represented. And among the aquatics, *Typha* and *Sparganium* were not found. Had these plants existed their pollen would very likely have been found for it is produced in large quantities and is of such a character that it is not likely

to be overlooked. Grasses are not represented but this may have been due to the inability of their pollen to be preserved in the shales in recognizable form, though it has frequently been recorded from Post-pleistocene deposits. The salt bushes (*Atriplex*), a genus of wind pollinated plants, abundant in the region at the present time, are not represented by pollen in the shales, nor are any other members of the Chenopodiaceae to which they belong, nor the allied family, Amaranthaceae. But the most significant of all is the entire absence of the great herbaceous family Compositae. Their pollen is among the most easily recognized, and is of such a character that it could scarcely have failed to be preserved, if present. The pollen of the entomophilous members of the group, it is true, might never have reached the lake, but it is scarcely possible that the anemophilous ragweeds or their allies could have flourished within miles of the lake and not have left their record in the shales by their pollen. Nor do we find represented the great anemophilous genus of the Compositae, the sagebrushes, which are abundant throughout the region at the present time. Both of these groups, in at least some of their species, delight in the conditions under which *Ephedra* flourishes, and if they had been present their pollen would have had a much better chance than that of *Ephedra* of reaching the lake, owing to the smaller size of their grains and more prolific production. Therefore we are forced to conclude that neither the ragweeds and their allies, nor the sagebrushes were represented in the flora of the Green River Epoch. In this connection it should be remembered that the Green River formation was laid down early in the Eocene period. Therefore the absence from it of terrestrial herbs is entirely in keeping with the thesis put forward by E.W. Sinnott, that the herbaceous type was developed in temperate regions during Eocene time in response to a progressive refrigeration. At this period terrestrial types were only beginning to be developed.

In closing I wish to thank Dr. E. D. Merrill and the staff of the New York Botanical Garden for the use of the herbarium, without which many of the identifications achieved would have been impossible. I am also indebted to Dr. E. W. Berry for much of the literature on Tertiary floras and for valuable suggestions. But especially am I indebted to the late Dr. Arthur Hollick with whom discussions of the various Tertiary floras were a frequent source of inspiration and encouragement.

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TABLE 1^a
List of families and genera represented in the Green River oil shales

	NUMBER OF SPECIES	IDENTIFICATION SOME- WHAT DOUBTFUL (X)	NUMBER OF SPECIES AL- READY KNOWN IN GREEN RIVER FLORA	POLLINATION BY WIND (W) BY INSECT (I)		NUMBER OF SPECIES	IDENTIFICATION SOME- WHAT DOUBTFUL	NUMBER OF SPECIES AL- READY KNOWN IN GREEN RIVER FLORA	POLLINATION BY WIND (W) BY INSECT (I)
Cycadaceae					Myricaceae				
Cycas	1		0	W?	Myrica	1		8	W
Dioon	1	x	0	W?	Salicaceae				
Coniferae					Salix	1		4	W-I
Abietineae					Betulaceae				
Pinus	3		1	W	Alnus	1		0	W
Picea	1		1	W	Betula	1		1	W
Abies	1		0	W	Carpinus	1		0	W
Cedrus	1	x	0	W	Ulmaceae				
(Abietipites)	1		0	W	Momisia	1	x	0	W
Tsuga	1		0	W	Simarubaceae				
Taxodineae					Ailanthus	1	x	1	I
Taxodium	1		0	W	Anacardiaceae				
Glyptostrobus	1		0	W	Rhus	1	x	5	I
Cunninghamia	1		0	W	Sapindaceae				
Gnetaceae					Talisia	1	x	1	?
Ephedra	1		0	W	Vitaceae				
Najadaceae					Vitis	1	x	0	I
Potamogeton	1		0	I?	Tiliaceae				
Arecaceae					Tilia	3		0	W-I
(Arecipites)	2	x	4	W?	Haloragidaceae				
Araceae					Myriophyllum	1		0	I?
Peltandra	1	x	0	I	Ericaceae				
Liliaceae					(Ericipites)	2		1	I
Smilax	3	x	0	I	Caprifoliaceae				
Magnoliaceae					Sambucus	1	x	1	I
Liriodendron	1		0	I					
Juglandaceae									
Hicoria	2		1	W					
Juglans	1		5	W					
Engelhardtia	1		0	W					

* This list should be compared with the list of the families and genera of the known Green River flora, compiled from Knowlton and Brown, and which has been published in the first article of the present series (46).

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RECENT PUBLICATIONS OF THE TORREY BOTANICAL CLUB

BOTANICAL results of the Tyler-Duida expedition, by H. A. Gleason, with the assistance of numerous collaborators. Reprinted from Bulletin of The Torrey Botanical Club, vol. 58. 230 pages, 29 plates, 8 figures, folding map, and special index. 1931. \$2.00.

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ARTHUR HOLLICK

(1857-1933)

ARTHUR HOLLICK

February 6, 1857—March 11, 1933

MARSHALL A. HOWE

WITH PORTRAIT

Although maintaining his youthful vigor in a large measure up to the last week of his life, Dr. Arthur Hollick, rounding out his three score and sixteen years, was, to many members of The Torrey Botanical Club, a link with the past. In company with his distinguished lifelong friend, Nathaniel Lord Britton, he joined the Club in October, 1877, when both were beginning their junior year in the School of Mines of what was then Columbia College. In his very interesting "Torrey Botanical Club Reminiscences," read on the occasion of the semi-centennial of the Club in 1917 and published in volume 17 of the *Memoirs*, he tells of his early habit of attending meetings of the Club in the City, missing the last (9 P.M.) boat to Staten Island, catching the midnight train on the Central Railroad of New Jersey, getting off at the Bergen Point Station, walking three quarters of a mile to the shore of the Kill van Kull, waking up the rowboat ferryman, and reaching home at Port Richmond about 1:30 A.M.! That was in the days when the election of a woman to membership in the Club would have been "unthinkable"! The enthusiasm for scientific activities thus manifested in his youth was destined to persist. On January 24, less than seven weeks before his passing, he had returned, with Mrs. Hollick, from a month's visit to Cuba, where he had engaged, in company with Brother León of the Colegio de la Salle, in an investigation of the fossil flora of that island, with the aid of a grant from the O. C. Marsh Fund of the National Academy of Sciences. During his month in Cuba, he visited localities in all six of its provinces, traveling more than one thousand miles, partly on horseback, and triumphantly bringing back to New York a large collection of excellently preserved plant remains, the critical study of which must now be given to others.

[Charles] Arthur Hollick was born at New Brighton, Staten Island, New York, on February 6, 1857, the son of Dr. Frederick and Eleanor Eliza (Bailey) Hollick. Both father and mother were English, coming to the United States in 1842 and settling on Staten Island. His father, left an orphan at four years of age, was thrown on his own resources

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when only thirteen, went from Claverdon to Birmingham, apprenticed himself to a silversmith, studied nights and attended lectures at the Mechanics Institute, receiving at seventeen a silver medal for proficiency in mathematics. At twenty-two he received the degree of M.D. from the University of Edinburgh. After coming to the United States he taught and lectured extensively on medical subjects, and was the author of several popular books on human anatomy and physiology. The elder Hollick was also a naturalist "of the old school," leaving collections of plants and minerals that are now in the possession of the Staten Island Institute of Arts and Sciences.

After preparation in private schools of New York and Wiesbaden, Germany, Arthur Hollick, then Charles Arthur Hollick, entered the School of Mines of Columbia College and on graduation in 1879 in the course in geology and paleontology received therefrom the degree of Bachelor of Philosophy. It is noteworthy that in 1879, the year of his graduation, "The Flora of Richmond County, New York," a pamphlet of thirty-six pages by Arthur Hollick of Port Richmond and N. L. Britton of New Dorp made its appearance. Hollick's first position, held for a short time, appears to have been that of Superintendent of the Mexican Mine in Mariposa County, California. In February, 1881, he was appointed Assistant Sanitary Engineer of the Board of Health of the City of New York, which consisted then of what is now the Borough of Manhattan and a part of what is now the Borough of the Bronx. During the ten-year period of his incumbency of this office, he was concerned especially with problems connected with factory vapors, water supply, sewerage, plumbing, ventilation, etc. On his inspection list during the process of construction were several important buildings, such as the old Madison Square Garden, the Mills Building, the Navarro Flats, etc. On one occasion, when the Board of Health was short-handed, as many as one thousand unfinished buildings were on his inspection list at one time. During this decade of his life, he was also a consultant or expert assistant in solving various sanitary problems of other municipalities, such as Brooklyn, Long Island City, Mount Vernon, Poughkeepsie, Elmsford, and certain communities on Staten Island. As late as 1910, he was asked to report on the geologic conditions affecting the water supply of Staten Island.

That Hollick's interest in plants was maintained during the ten years that he was primarily engaged in sanitary engineering is evidenced by the publication of notes and reviews in the BULLETIN OF THE TORREY BOTANICAL CLUB, especially perhaps by the several lists of "Additions and New Localities" to the Hollick and Britton "Flora of Richmond

County" [Staten Island]. His interest is further attested by the fact that he served as Recording Secretary of the Club for the years 1883 to 1888, inclusive, and later as an Associate Editor of the *BULLETIN*. His more strictly and actively scientific career began with his appointment in 1890 as Fellow in Geology in Columbia College, to which position he was reappointed in 1891. He had previously acted from time to time as a private assistant to Professor J. S. Newberry and had made the drawings for many of Professor Newberry's published papers on fossil plants and fishes. In the college year 1891-92 he carried on a part of the lecture work of Professor Newberry, then incapacitated by illness, and in 1892 he was appointed Assistant in Geology. In that year he conducted the summer school of geology for the third-year students in mining engineering at the Lake Superior mines. This is said to have been the first attempt at practical field geology in the history of the School of Mines. In 1893 his title was changed to Tutor in Geology. At this time and later he gave instruction in drawing to Columbia college students in various courses in geology and paleontology. During this period he was carrying on research work that was accepted by the Columbian (now George Washington) University in fulfillment of the requirements for an advanced degree and in 1897 the degree of Doctor of Philosophy was conferred upon him by that institution. In 1900, Dr. Hollick conducted the Summer School of Geology at Canyon City, Colorado.

Another epoch in the career of Dr. Hollick began on July 1, 1901, when (at the same time as the writer of the present sketch) he became an Assistant Curator of The New York Botanical Garden, which meant that he was placed in charge of the collections of fossil plants, with a considerable amount of his time free for research. The Garden's collection of fossil plants was at that time essentially non-existent, but by a previous agreement between the Board of Managers of the Garden and the Trustees of Columbia University, the paleobotanical collections of the University were soon deposited in the Museum Building of the Garden, under terms of agreement similar to those under which the general herbarium of Columbia University had already been deposited at the Garden. The Columbia collection of fossil plants consisted of several thousand specimens, including the types of many species described by Professor Newberry. In 1901, Dr. Hollick spent a month in Maryland, in coöperation with the Maryland Geological Survey, collecting fossil plants that were described by him in 1906 in the "Pliocene and Pleistocene" volume of the Maryland Geological Survey. In 1903 he spent four months in Alaska under the auspices of the United States Geological Survey,

exploring the Yukon River Valley, going down the river by canoe from Dawson to Anvik, a distance of more than 1000 miles and bringing back to Washington 1800 pounds of specimens. Later, he was in residence in Washington for two periods of six months each, studying the Alaskan material obtained on this trip and preparing reports upon it for the United States Geological Survey. His general scientific activity in the period from 1901 to 1914 is reflected in numerous titles in the bibliography published below. Noteworthy are his articles on "Palaeobotany" in volume 13 of *The New International Encyclopaedia* (1903) and on "Palaeobotany or Fossil Botany" in volume 11 of the *Encyclopaedia Americana* (1904).

Arthur Hollick was one of the prime-movers in the establishment of the Natural Science Association of Staten Island (later the Staten Island Association of Arts and Sciences and finally the Staten Island Institute of Arts and Sciences). With N. L. Britton and William T. Davis, he signed the call for a meeting on Nov. 12, 1881, to organize a scientific society on Staten Island. At this organization meeting he was elected corresponding secretary, a position afterwards merged with that of secretary, to which post he was elected in January, 1893. From 1883 to 1888, he was co-editor of the *Proceedings of the Association* with William T. Davis, and from 1888 to 1892 he was the sole editor. It is said that he attended the meetings of the Association, rain or shine, and that from the initial meeting in November, 1881, to November, 1893, he missed only two meetings, one on account of illness and one by reason of being in the Rocky Mountains region at the time. In the reorganization and incorporation under the name of the Staten Island Association of Arts and Sciences in 1904 and 1905, Dr. Hollick became Recording Secretary and a member of the Board of Trustees. In November, 1913, he tendered his resignation as a member of the curatorial staff of The New York Botanical Garden, effective December 31, to accept the position of Curator-in-Chief of the Public Museum of the Staten Island Association of Arts and Sciences, a title that soon thereafter was changed to that of Director. In resolutions expressing regret at his withdrawal, the Scientific Directors of the Garden recognized his "enthusiasm and ability" and his noteworthy investigations "highly creditable to himself and to the Garden" and voiced a request that the Board of Managers should designate him as Honorary Curator of Fossil Plants, a request with which the Managers soon complied. On May 17, 1919, Dr. Hollick resigned the directorship of the Staten Island Museum and in 1921 he was again a member of the curatorial staff of The New York Botanical Garden, with the title of Paleobotanist, a position that he held until his death on March 11, 1933, though on July 1, 1932, his title was changed to Research Associate in Paleontology.

In 1926, Dr. Hollick spent a large part of the month of March in Porto Rico. The results of his investigations there were published in 1928 in volume 7 of the Scientific Survey of Porto Rico and the Virgin Islands, his report on the Paleobotany of Porto Rico covering 228 pages and including 38 plates. Four years previously he had published "A review of the fossil flora of the West Indies, with descriptions of new species," the newly described forms being mostly from Porto Rico, Trinidad, and Cuba. Other important paleobotanical contributions of Dr. Hollick during the last decade of his life are "The flora of the Saint Eugene silts, Kootenay Valley, British Columbia," 1927, and "The Upper Cretaceous flora of Alaska," 1930, the latter with 87 plates. What may fairly be considered Hollick's *magnum opus*, his report on "The Tertiary flora of Alaska," remains unpublished in the files of the United States Geological Survey in Washington. This consists of 723 typewritten pages and 121 plates.

In addition to the scientific organizations already mentioned, Dr. Hollick was a charter member and for several years Treasurer of the Botanical Society of America, a Fellow of The New York Academy of Sciences, the Geological Society of America, and the American Association for the Advancement of Science.

Any record of the life and career of Arthur Hollick would be incomplete without some record of his activities as a citizen interested in good government. From 1886 to 1892 he was a member of the Board of Health of the village of New Brighton on Staten Island, being especially active in securing frequent analyses of drinking water, in the establishment of a sewerage system, and in abating the smoke nuisance caused by factories in Bayonne, N. J. Governor Black, in 1897, appointed him a member of Board of Park Commissioners for Richmond County, of which he was made vice-president and later (1901-1904) president. In 1900 he helped to organize the Richmond Borough branch of the Citizens Union and was one of the vice-presidents of the Fusion meeting that resulted in the nomination of Seth Low, President of Columbia University, as Fusion candidate for Mayor of Greater New York, and he was a member of the special committee that notified Mr. Low of his nomination. After the election of Mayor Low in 1901, he remained active in the Citizens Union organization. In 1906, Mayor George B. McClellan appointed him a member of the Board of Education of the City of New York.

On September 19, 1881, Arthur Hollick married Adeline Augusta Talkington. A golden wedding celebration was held on Staten Island in September, 1931. Besides his widow, Dr. Hollick leaves two daughters, Eleanor Adeline (Mrs. Eleanor H. Wells) and Grace Eaton (Mrs. R. H.

Pentz) both residents of St. George, Staten Island, and several grandchildren. A son, Roger Frederick, died in early manhood.

Arthur Hollick was a man of broad interests, keeping in touch with the best in English poetry and prose; an enthusiastic devotee of golf and bowling; a productive scientist of wide range; an excellent lecturer; a man of a sensitive responsive nature; a man with the instincts of a gentleman and, withal, a man whom his associates will miss.

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THE NEW YORK BOTANICAL GARDEN

The curvature, symmetry and homologies of the sporocarps of *Marsilea* and *Pilularia*

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(WITH PLATE 26)

The prime purpose of this paper is the correction of two errors that are almost universally made in describing the sporocarp of *Pilularia*. In the first place, while all current handbooks of the ferns, *quite correctly*, designate sections of the capsule of *Marsilea* that are perpendicular to the sagittal plane and parallel to the axes of the sori as *transverse sections*, like sections of *Pilularia* are everywhere called *longitudinal*. The latter designation is clearly quite erroneous from a morphological standpoint. A second mistaken assumption, made in practically all the handbooks is the assumption that the capsule of *Pilularia* is radial in its symmetry. The unfortunate results of these two misconceptions are that a detailed comparison of these two sporocarps and so the recognition of their very close homology has proved impossible.

A chief reason for the first error mentioned regarding the structure and homology of the mature sporocarp of *Pilularia* is the difference in the amount and the persistence of the curvature of the peduncle, in *Pilularia* itself and in the different species of the related *Marsilea*. The comparison of the development of the sporocarps in several species of these two genera makes clear the very exact homology between them, and the causes of the above-mentioned errors also become evident.

In the sporocarp of *Marsilea quadrifolia*, e.g., the development of this structure from a bifacial initial cell is known in more detail than for any other member of the genus. The youngest sporocarps of this species seen were nearly straight (Johnson, 1898,¹ fig. 25). Later the more rapid growth of the dorsal side of the peduncle, just below the capsule, bends the peduncle through almost 180°, which brings the ventral side of the capsule to lie nearly in contact with that of its own peduncle (Johnson, 1898,¹ fig. 31a). In consequence of this its soral canals, from pointing perpendicularly away from the axis of the peduncle, come to point directly toward the basal part of the peduncle. The capsule itself, meanwhile, remains practically straight. As this sporocarp matures the U-bend of the peduncle unbends through 90° or more, till the long axis of the ripe capsule, instead of being parallel to its own peduncle, comes to make a wide angle, often as great as 120°, with its own stalk. The soral canals thus come to point not toward the peduncle, but outward and downward at an angle of some 30° with it. The apical region of the capsule is at the end opposite that to which

¹ Botanical Contribution from the Johns Hopkins University, No. 120.

the peduncle is attached. This is the position of the capsule on the peduncle when the sporocarp is mature (fig. 3. cf. Alex. Braun, 1870, p. 702, fig. 3; Johnson, 1898,¹ fig. 44).

If now we compare the capsule of *Pilularia globulifera* with that of *Marsilea quadrifolia* we find that the peduncle of this *Pilularia* also bends markedly, just where it does in *Marsilea*,—but it bends in the *opposite* direction. When very young the sporocarp of this *Pilularia* is straight and when the soral canals are initiated they point, just as in *Marsilea*, ventrally and at right angles to the straight common longitudinal axis of the peduncle and of the capsule itself (fig. 4). Later, as the peduncle and capsule become more clearly differentiated, the peduncle begins to curve backward and it continues this until maturity, when its form becomes fixed (figs. 5, 6). The curvature here is far less than the primary curvature in *Marsilea*. In fact the change in direction of the soral axes is rarely more than 60° instead of the 180° of *Marsilea quadrifolia*. Finally there is no reversal of this primary curvature in this *Pilularia* such as we saw in *Marsilea*. The result of this bending in *Pilularia*—one is inclined to call it a straightening out, when seeing the relation of capsule to peduncle at maturity—is that the outer ends of the 4 soral canals come to have a nearly terminal position. In other words, their axes make an angle (on the ventral side) of 160° with the peduncle and so come within 15 or 20° of being parallel to the axis of the peduncle. But the canals point upward, not downward as in *Marsilea* and the apical region of the capsule (location of initial cell) is directed backward and upward at an angle of 130° with the peduncle (fig. 6 at A). It is because of this curvature of the peduncle of *Pilularia globulifera* that sections of the capsule cut perpendicular to the soral canals have been, quite erroneously, thought of as *transverse* sections and so labelled in all the handbooks. They are in reality nearly longitudinal and horizontal ones morphologically. (Fig. 7 “MN”). For the same reason sections parallel to these canals and perpendicular to the sagittal plane are *transverse not longitudinal*—in the same sense as in *Marsilea* (Figs. 10, 11, 12 cf. Johnson, '98,¹ Figs. 31, 32, 33). Nevertheless such sections of *Pilularia* are labeled *longitudinal* in all the handbooks (e.g. Luerssen, fig. 191, p. 617; Meunier, 1887, figs. 12, 13, 53; Engler and Prantl, 1902, figs. 227, 229B; Lotsy, 1909, figs. 427, 428; Bower, 1926, fig. 463; Goebel, 1882, figs. 2, 7, 8; Campbell, 1918, figs. 254^E, 256A; 1893, p. 143 and figs. 4, 6, 8, 9).

In a *Pilularia* recently collected in Venezuela by Pittier, (probably *P. americana*) the mature sori make an angle of but 75° or 80° with the peduncle instead of the 160° we have found in *P. globulifera*. That is, there is no such considerable bending backward or “straightening out” of the

peduncle of this species as there is in *P. globulifera*. If, which is probable, the soral canals are lateral in origin, as in *P. globulifera*, there must in this species be a slight bend forward of 10° or 15° instead of the marked backward bend of the peduncle found in *P. globulifera*. There can hardly be so strong a forward bend as is stated by Campbell (1893, p. 142).

In *Pilularia minuta*, which I have recently been able to study, the capsule itself develops much as in *P. globulifera*. The soral canals at first point ventrally but the curving of the peduncle is here a strongly hypostastic one, which brings the two soral canals of this species to point downward toward the very base of the peduncle. This brings the originally apical region of the capsule to face perpendicularly away from the peduncle against which its basal side lies. It is evident then that transverse sections of the mature capsule of *P. minuta*, i.e. sections parallel to the soral canals and perpendicular to the sagittal plane, will be in a plane nearly parallel to the peduncle. But the soral canals here point downward, not nearly upward from the peduncle as in *P. globulifera* (figs. 8, 9, 10). On the other hand, morphologically longitudinal sections of the capsule, i.e. those perpendicular to the soral canals, are actually transverse to the peduncle (Johnson 1933¹ figs. 14, 16, 19, 22, 28). None of the mature capsules of my material were erect, as they were reported to be in this species by Alex. Braun. In the degree and direction of curvature of its peduncle then *P. minuta* differs markedly from *P. globulifera*, and also from *P. americana*. Moreover, the first bending of the peduncle in all three species of *Pilularia* is permanent. There is no reversal of the bending, such as occurs in *Marsilea quadrifolia*.

In general then wherever sections along the soral canals of *Pilularia minuta* or *P. americana* have been illustrated in monographs or handbooks, they have been mistakenly called *longitudinal*, even where they were directly compared with similar sections of *Marsilea* which were labelled *transverse*. This error has evidently been due to the assumption that these capsules correspond in *every way* to that of the wrongly interpreted one of *P. globulifera*.

! Much this same diversity, in the degree of curvature of the peduncle, that we have described for *Pilularia* is also found in the different species of *Marsilea*. Thus while the angle between the peduncle and the axis of the sorus in *Marsilea quadrifolia* is about 30° ; in *M. nardu* this angle is 40° and finally in *M. salvatrix* it is nearly or quite 90° and the peduncle is attached to the middle of the end of the capsule. In *M. polycarpa* on the other hand, as figured by Alex. Braun, the axis of the sorus becomes nearly parallel to the peduncle showing a forward curvature of 90° , while in *M. Brownii* the peduncle appears never to have straightened out at all from

its first curvature and the soral canals point downward and inward toward the base of the peduncle. (figs. 13, 14, 15, 16.) The mistaken interpretation of the structure of the capsules of the *Pilularia* referred to above would probably not have been made so generally if their capsules had been compared with those of several species of *Marsilea* instead of with that of *Marsilea quadrifolia* alone.

In the third genus of the Marsiliaceae, *Regnellidium*—as figured by Lindman—the angle between peduncle and soral axis is 90° . Moreover this capsule appears as if attached to the peduncle by its long (dorsal) side and not by its end as it is in *M. salatrix* referred to above. (See Lindman, 1904, fig. 3^A).

SYMMETRY OF THE CAPSULE OF PILULARIA

The second mistaken conception referred to regarding the capsule of *Pilularia*, namely that it is radial in symmetry, is readily proved erroneous by a study of the development of the sporocarps of either of the three species referred to above. Such a study shows at once that the sporocarps of *P. globulifera* and *P. minuta* (and so probably those of all other species) are from the first *zygomorphic*, or *bilaterally symmetrical* structures. They are closely identical in fundamental plan with that of *Marsilea quadrifolia*. Thus the capsule of *P. globulifera* is developed from a bifacial initial cell, the approximately semicircular segments of which meet at the “median wall” which latter is clearly seen in all sections of the young capsule that are either transverse or horizontal. This apical cell which is at first terminal, is gradually pushed around toward the dorsal side by the more active elongation referred to above, of the ventral side of the capsule (figs. 4, 5, 6). The four sori, as are those of *P. americana*, are distributed two on each side of the median or sagittal plane of the capsule. There is a marked pit and a tubercle on the midline of the dorsal surface of the capsule, just above where the peduncle joins it (Johnson, 1898,² Fig. 33). Internally there is an overlap of two layers of the hypodermis, a right angle bend and a Y-like forking of the vascular bundle of the peduncle, and a sclerenchyma strand lying against the ventral face of this bundle. All of these internal structures also lie in the sagittal plane of the fruit, and so serve to further emphasize its bilateral symmetry.

The sporocarp of *Pilularia minuta*, is, like that of *P. globulifera*, evidently due primarily to the activity of a two-sided initial cell, like that actually seen in its young leaf (Johnson 1933, figs. 6, 8). This is indicated: (1) By the clearly marked “median wall” in its capsule, that is seen in each transverse and each horizontal section; By the plan of its capsule, which has one sorus and one soral canal in each half; (figs. 7, 8, 10), by its

vascular bundle which splits to a right and left fork just after entering the capsule. All these *paired* structures show this capsule to be *bilaterally symmetrical* (See Johnson, 1933, figs. 18, 25, 27, 28). *Another series* of *unpaired* structures, all of them located on the midline of the dorsal (abaxial) surface of this capsule, emphasize still further its zygomorphic or dorsiventral symmetry (fig. 9). These include: the external tubercle, of decidedly specialized internal structure; (1933, figs. 22, 39); the "pit" just above this tubercle; the *overlap* of two narrow flaps of the thickened hypodermis (See Johnson, 1933, figs. 39-42) and the right angled bend of the vascular bundle as it enters the wall of the capsule, just below this overlap.

Each of the structural features of the capsule of *Pilularia minuta* referred to in the last paragraph, the paired and the unpaired ones, has its close counterpart in the capsule not only of *Pilularia globulifera*, but likewise in that of *Marsilea quadrifolia*.

From all the facts given above regarding the sporocarps of these two genera, it is clear that these are, from the beginning of their development, zygomorphic or bilaterally symmetrical structures. This is true of both peduncle and capsule (See Johnson, '98,² pp. 7, 11). The existence of this type of symmetry in the sporocarp of *Marsilea* has long been generally accepted (Mettenius, 1846, p. 33; Alex. Braun, 1870, p. 696). Braun and Goebel, however, seem to be the only students of *Pilularia* to suggest the occurrence of dorsiventral symmetry in the sporocarp of *Pilularia*. Braun (1870, p. 706) gives no detailed statements of the evidence for this view but, after stating categorically that the capsule of *Marsilea* has a dorsal and a ventral side, he merely adds—"und nach der Nervatur möchte ich dasselbe von *Pilularia* glauben." Braun, though he does not say this, probably thought of the plane of symmetry as passing through the stalk and as separating the two arms of the basal fork of the vascular bundle, which bundle he actually figured (Braun, 1870, p. 705, fig. 3). Whether he, as later writers have done, regarded the region of the mature capsule which is nearly opposite the point of its insertion on the peduncle as the morphological apex of the sporocarp is not entirely clear. But this seems probable from his statement regarding the position of the sori in the capsule of *Pilularia*, of which he says (Braun, 1872, p. 678) "Sori in sporocarpio globoso *longitudinales*." In contrast he says of *Marsilea*—"Sori in sporocarpio zygomorpho *transversales* pinnatim disposita." (Braun, 1872, p. 668). These two statements seem to show that he regarded the plan of the sporocarp of *Pilularia* as different from that of the "zygomorphic" *Marsilea*. At all events, the view that regards the end of the mature capsule of *P. globulifera* opposite the point of its insertion on the peduncle

as the morphological apex of the capsule, is the view which has been practically universally accepted by later workers. This is probably due to the fact that in this species the axes of the originally transverse sori came, finally, to lie nearly in line with the peduncle. Thus Goebel (1882, p. 777) says "a cross section of a young *Marsilea* fruit is strikingly like a longitudinal section of a *Pilularia* fruit." In his Plate IX, Fig. 2, he designates a section of the capsule of *Pilularia* at right angles to the soral canals as a *transverse* section. Even in the last edition of the *Organographie der Pflanzen* (Goebel, 1930, p. 1286) speaks of a section perpendicular to the soral canals and the meridional vascular bundles of *P. globulifera* as *transverse*. Elsewhere in this volume (p. 1281) Goebel does speak of the sporocarp of *Marsilea* and *Pilularia* as always dorsiventral but, he gives no evidence to support this and later remarks that in *Pilularia* this symmetry *is not evident externally*. Meunier (1887, figs. 13, 47, 50) and Campbell (1893, p. 142) evidently regard the capsules of *P. globulifera* and *P. americana* respectively as radial in symmetry. Thus Meunier (1887, pp. 359, 360) says each of the 4 lobes of the sporocarp, one "above" each sorus, has a separate initial, which is said to arise independently, *after the initial of the sporocarp as a whole has ceased to function*. He gives as a typical longitudinal section of the sporocarp (1887, fig. 12) one diagonal to the sagittal plane which thus passes through the middle of one sorus in the left half of the capsule and of another in the right half, and misses altogether the tubercle, the pit and the overlap of the hypodermis, all of which, as we have seen, lie in the median plane. Campbell on the contrary, (1893, p. 142) thinks the original apical cell of the whole sporocarp occupies the tip of *one* of the *four* lobes, while the *other three arise separately*:—one on a line directly below the initial and one on each side of this line. If this were true, the plane of symmetry must really, of course, pass through the first two lobes mentioned and so through two diagonally opposite sori of the mature capsule. Lindman (1904, p. 9) contrasts his new genus *Regnelidium*, which he says is bilaterally symmetrical like *Marsilea*, with *Pilularia*, in which latter he says the sori are "whorled."

All these views of the symmetry and of the origin of the lobes of the sporocarp of *Pilularia* are, as a matter of fact, erroneous, as was shown by a detailed study of the development of the capsule of *Pilularia globulifera* (Johnson, 1898,² pp. 7, 18–22, figs. 14, 24, 31, 33). A recent study of the development of the sporocarp of *Pilularia minuta* has confirmed the results and the interpretations published earlier regarding *P. globulifera*. The prime differences between the capsules of these two *Pilulariae* and that of *Marsilea quadrifolia*, as shown by the two studies mentioned, are in the number of sori formed on each side of the midplane and in the posi-

tion of the mature capsule on the peduncle. In all other essential details of structure the mature capsule of a *Pilularia* corresponds with that of a *Marsilea*. Moreover, the sporocarp of *Pilularia* is like that of *Marsilea* in being developed by the activity of a single, bifacial initial, with convex faces.

Another question regarding these genera that is not yet settled to the satisfaction of all workers is that of the homologies between the sterile and fertile divisions of the leaf—the foliage leaf and the sporocarp. The generally accepted view is that the sporocarp is a fertile portion (“lobe” or “leaflet”) of the leaf or frond, comparable with the fertile portion of the sporophyll of e.g. an *Aneimia* or *Lygodium*. This has led to the further assumption that the sporocarp of *Marsilea* or *Pilularia* is a fertile pinna, comparable except for its sporangia with one or more of the 4 terminal leaflets of the sterile leaf of *Marsilea* (See Goebel, 1882, p. 773; 1930, pp. 1283). The occurrence in a longitudinal series of the 10 or 15 sporocarps of *M. polycarpa* is often cited as convincing evidence that these are equivalent to the pinnae of a once-compound fern frond. Thus Goebel (1930, p. 1283) regards each sporocarp of *Marsilea* as a single pinna. Campbell, on the other hand, (1893, p. 143) says the 4 prominences on the young capsule of *Pilularia*, one for each locule, “are beyond doubt to be regarded as 4 leaflets,” and says the ripe capsule splits to 4 valves corresponding to these lobes or leaflets. Even in his latest work on this form (Campbell, 1918, p. 435) seems still to hold to the above mentioned interpretation. His view, stated above, is that one of the lobes or pinnae, which he thinks composes the capsule, arises from the original initial of the sporocarp and a second one on the mid-line of the ventral surface. Both these suggested modes of origin of a “leaflet” are quite different from the origin found in *Marsilea* and from any known in any related fern.

Bower in speaking of the homology of the capsule of *Marsilea* says (Ferns II, 1926, p. 188)—“the hypothesis seems tenable that the sporocarp (capsule) consists of a rachis bearing two rows of pinnules: this is indicated by the venation.”—This view is like that of Campbell in regarding the capsule as composed of several pairs of pinnae fused into one structure.

Before any one of these views can be accepted, however, it must be shown that it is in accord with certain known facts concerning the structure and development of the sporocarps of *Marsilea* and *Pilularia*. We have seen that the sporocarp of *Marsilea* is initiated like that of *Pilularia* by a single, bifacial initial with convex faces. In other words, the initial of the sporocarp is precisely like that of the leaf as a whole (See Johnson, 1898,¹ figs. 4, 18, 21, 34). The pinna of the sterile leaf of *Marsilea* on the contrary is formed by the activity of several to many 5-sided marginal cells, each

like a 100° sector of a disk, whose thickness is about $1/5$ of its diameter (Johnson, 1898,¹ figs. 19, 20). Though the sporocarp may ultimately be shown to be a fertile pinna, the writer can see no evidence from these facts of development for so regarding it. Another clear indication that the sporocarp is often something more complex than a single pinna, or a group of fused pinnae of one order, is the fact that the primary sporocarp of a leaf may often give rise to a secondary sporocarp from an initial arising in a marginal cell of the stalk of the primary one. Not infrequently a tertiary one also may arise thus from the peduncle of the secondary sporocarp. For those who think of the sporocarp as a pinna, these instances, which they seem to have overlooked, must be regarded as cases of twice or thrice compound foliar structures. Such an interpretation does not, to say the least, make it any easier to settle the homology between the sporocarp and the sterile segment of its own leaf or the affinities of the Marsileaceae with those other Filicales such e.g. as the Schizaeaceae with which they have been thought to be related.

SUMMARY AND CONCLUSION

The sporocarps of the *Pilulariae* like those of the *Marsileae* are shown by their development to be zygomorphic structures; i.e. they are bilaterally symmetrical with reference to a *median* or *sagittal* plane.

The paired young soral canals open, in all cases, one of each pair on each side of the midline of the ventral face of the capsule.

The tubercle, pit, overlap of the hypodermis, and Y-like forking of the vascular bundle *all* lie in the midplane of the capsule.

The bending of the peduncle is always in this same plane—the sagittal one.

The *direction* of the primary bending is different in *Marsilea quadrifolia* and *Pilularia globulifera*, being hyponastic in the former and epinastic in the latter.

The amount of the bending is relatively constant for each species, but differs strikingly in different species of each genus.

The bending is sometimes permanent at the farthest limit reached, while in other cases the primary bending may be largely reversed or “unbent” before the capsule matures.

If the zygomorphic symmetry of the sporocarp of *Pilularia* is not forgotten, as it usually has been when comparing it with *Marsilea*, it becomes clear that its capsule is very closely equivalent to that of *Marsilea* except that it has but two pairs of sori in each half in *P. globulifera* and but one sorus on each side in *P. minuta*, instead of six or more sori in each half of the capsule, that are found in *Marsilea quadrifolia*.

The details of development of the sporocarp in both *Marsilea* and *Pilularia* and the occurrence of secondary, and even tertiary sporocarps in *Marsilea* seem to give no support to the view that the sporocarp of the Marsileaceae is to be regarded as a fertile pinna equivalent in origin to the sterile leaflet of *Marsilea*.

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Explanation of plate 26

Fig. 1. Right side of young leaf of *Marsilea quadrifolia* bearing very young, slightly bent sporocarp. $\times 11$.

Fig. 2. Right side of somewhat older sporocarp of *M. quadrifolia* showing apex of capsule bent down against base of its peduncle. $\times 15$.

Fig. 3. Inner surface of left valve of mature, emptied capsule of *M. quadrifolia* showing outline, with pit and tubercles, the vascular system and the internal structure of the basal region of the capsule. $\times 6$.

Fig. 4. Ventral surface of very young sporocarp of *Pilularia globulifera* showing its bilateral symmetry, the initial of the sporocarp and those of the sori. $\times 170$.

Fig. 5. Approximately sagittal section of a half-grown sporocarp of *P. globulifera* passing far enough to the right of the median plane to cut through the two sori of the right half of the capsule. $\times 170$.

Fig. 6. Median sagittal section of a ripe capsule of *P. globulifera* passing through the indusium between the two sori of the left half and the two of the right half of the capsule. $\times 13$.

Fig. 7. Left side of a half-grown sporocarp of *Pilularia minuta* (cleared in glycerine) showing outline of capsule, sporangia, basal wall and peduncular vascular bundle. $\times 80$.

Fig. 8. Abaxial (apical) face of nearly mature capsule of *P. minuta* showing bilateral symmetry as indicated by its soral papillae and position of sporangia. $\times 25$.

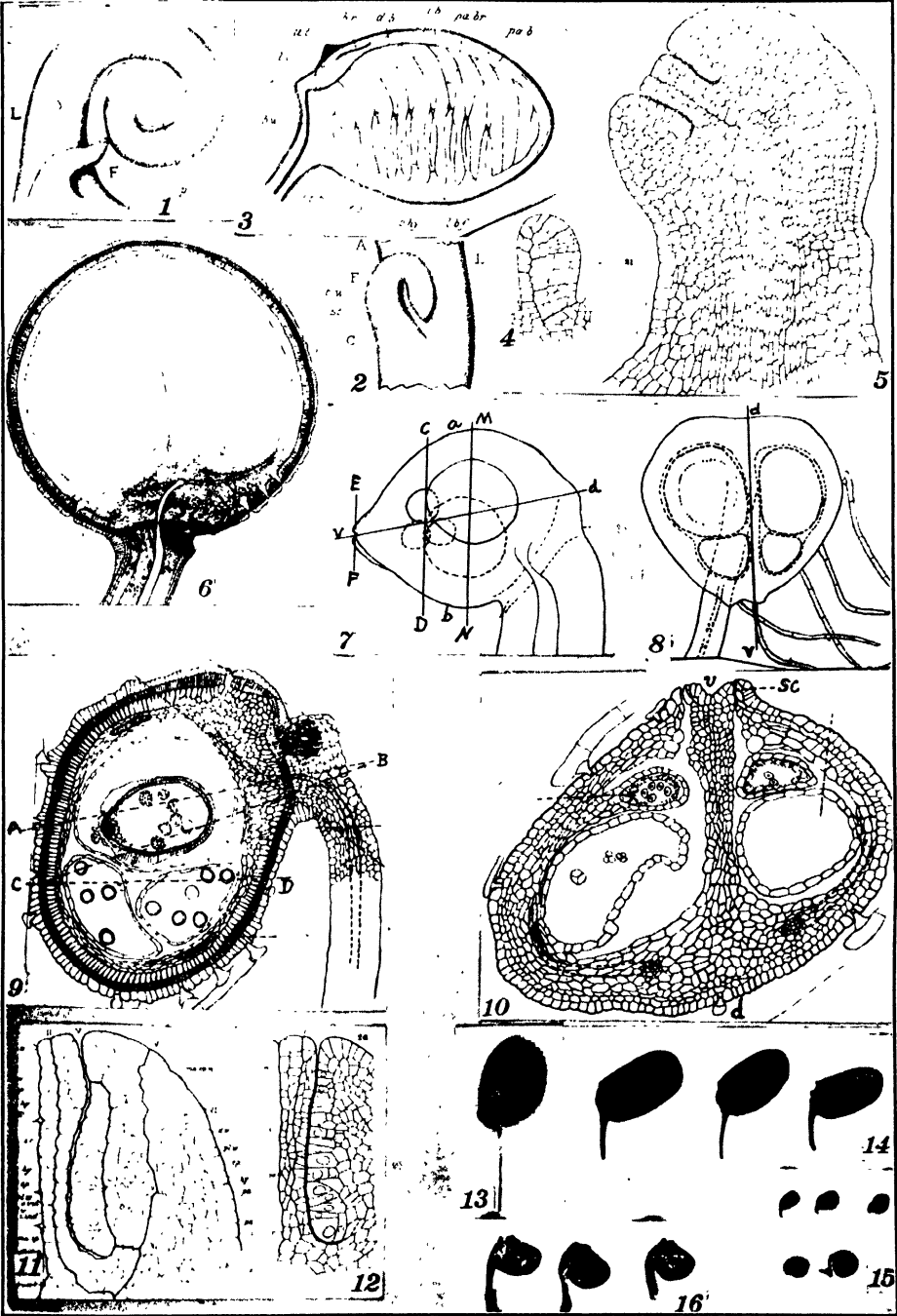
Fig. 9. Nearly sagittal section of mature capsule of *P. minuta* showing outline, including pit and tubercle; also course of vascular bundle, overlap of hypodermis in basal wall and the relative position of the micro- and megasporangia in the right sorus. $\times 50$.

Fig. 10. Transverse section of a half-grown capsule of *P. minuta* (along line "dv" of Fig. 7) indicating the bilateral symmetry by the paired soral canals and papillae and the micro- and megasporangia of right and left locules. $\times 100$.

Fig. 11. Part of a transverse section of a young capsule of *Marsilea quadrifolia* through (and longitudinal to) a soral canal and a sorus with 4 megasporangium initials. $\times 230$.

Fig. 12. Part of a transverse section of a young capsule of *Pilularia globulifera* showing soral canal and sorus with megasporangium initials. Note identity of position of these structures with those of *Marsilea* shown in Fig. 11. $\times 180$.

Figs. 13-16. Lateral views of the capsules respectively of *Marsilea salvatrix*, *M. nardu*, *M. polycarpa* and *M. Brownii* showing in each the position of the capsule in relation to the peduncle and in Fig. 14 the direction of the sori in the capsule. $\times 1\frac{1}{2}$.



JOHNSON: MARSILEA AND PILULARIA

The constancy of cultural characters and pathogenicity in variant lines of *Ustilago zeae*¹

E. C. STAKMAN, L. J. TYLER, AND G. E. HAFSTAD

(WITH PLATES 27 AND 28)

In 1929 Stakman, Christensen, Eide, and Peturson² published the results of extensive studies on mutation and hybridization in *Ustilago zeae* (Beckm.) Ung. It was shown that some unisexual lines, therefore presumably haploid, produced large numbers of new lines as a result of sectoring in colonies growing on artificial media in Erlenmeyer flasks. It was argued that the origin of the new lines could best be explained on the basis of mutation, although it was admitted that an unusual type of segregation also might be responsible. In any case, the change seemed to be genotypic, as the new characters were relatively constant and there was evidence from studies on hybridization that the changes involved the nucleus. The writers now are making studies designed to elucidate some of the problems involved. In the meantime, further evidence of constancy of "mutant" characters has been obtained.³ As the results seem significant, they are presented in this paper.

A special study was made of the degree of constancy of cultural characters and pathogenicity of several "mutant" lines of "W. Va. A8" isolated in 1928 and grown on artificial media since that time. The early history of some of the lines is given in a previous publication² (P.1, p. 10-14, and fig. 1). W. Va. A8 was isolated from a collection of smut obtained from Dr. R. J. Garber of West Virginia. Several monosporidial isolations were made in January, 1928, and, as the cultures developed from them appeared alike, one line was selected for further study. From this monosporidial line 162 variants were isolated by the fall of 1928, and some have been kept continuously in culture since they first appeared. Most of those discussed in this paper were isolated in the early spring of 1928, although some appeared during the summer; hence the lines are now from $4\frac{1}{2}$ to 5 years old.

Some of the lines have produced numerous sectors, but, despite this

¹ Paper No. 1175 of the Journal Series of the Minnesota Agricultural Experiment Station. Supported in part by a grant from the Graduate School of the University of Minnesota.

² Stakman, E. C., J. J. Christensen, C. J. Eide, and Bjorn Peturson. Mutation and hybridization in *Ustilago zeae*. Minn. Agr. Exp. Sta. Tech. Bul. 65. 1929.

³ Stakman, Christensen, Eide, and Peturson designated as mutants the variants that arose as sectors, although they qualified the term (Minn. Tech. Bul. 65, p. 53 et seq.). The present writers also think there is good evidence that new lines arise through mutation, but there remains the possibility of delayed segregation. Therefore the term variant is used, but the viewpoint remains the same.

fact, it has been possible to maintain the original types in culture by the simple expedient of growing the cultures in flasks and transferring from the parental type and from the sectors separately. Some of the lines that do not sector abundantly were grown in tubes much of the time, only occasionally in flasks; and all of them were grown in tubes some of the time. As it is difficult to detect sectors in tubes, it seems all the more remarkable that the original types were maintained for a period of approximately five years.

Fourteen of the lines of the W. Va. A8 series have been grown periodically in duplicate or triplicate flasks on several kinds of media. They were always distinct from each other in appearance, and, by comparing their characters with those recorded in descriptions and photographs about five years ago, it is evident that they are as nearly identical in appearance with the original cultures as could be expected under the circumstances. For it is, of course, impossible to duplicate exactly the conditions under which cultures are grown four or five years apart, and the cultural characters of a line may vary considerably with composition of medium, temperature, moisture, light, and other environmental factors.

In plate 27 are shown 8 lines, all of them isolated about four and a half or five years ago, except A8-10-1 and A8-3-1-1, which appeared more recently as sectors in colonies of A8-10 and A8-3-1, respectively. As some of the lines differ from each other in color, the differences do not appear as distinct in the photograph as they actually are. The plate does show, however, that the eight lines, all of them descendants of a single unisexual sporidium, were still different from each other when photographed in October, 1932.

Plate 28 shows that the lines not only differ from each other but that they also have retained their distinctive characters. The plate was made from a combination of photographs taken at different times. On the left are shown cultures of three lines on potato dextrose agar, photographed in September, 1929; in the middle, cultures of the same lines on potato dextrose agar, photographed in October, 1932; and on the right, the same lines on potato malt agar, photographed in December, 1932.

Each vertical series shows the differences between the three lines at a given time and on the same medium, while each horizontal series shows the range of variability in the appearance of colonies of one line at different times and on different media. As the photographs were taken at different times and the enlargement is not the same in all cases, the differences in the appearance of colonies of the same line are somewhat accentuated. Despite the variability, certain characteristics of color, topography, margin, and surface markings distinguish each of these lines, as well as the others, when grown under reasonably uniform conditions.

Stakman, Christensen, Eide, and Peturson⁴ emphasized the fact that there may be great phenotypic variability in cultures of monosporidial lines, but that the lines are constant genotypically except as new ones arise through what appears to be mutation. The accuracy of this conclusion is attested by a study of Plate 28. There is considerable variability in the appearance of cultures of each line. This is accounted for partly by the fact that the 1932 series on potato dextrose agar grew during August and September, when the weather was extremely hot. The agar therefore dried out unusually rapidly and the colonies were somewhat subnormal in size and not so characteristic in appearance as usual. The colonies on potato malt agar, grown later in the fall, are of about average size, and the difference in their appearance is what would be expected on this medium. It is important to bear in mind, therefore, that the three colonies of each line grew under quite different conditions. Considering this fact, the resemblances are striking. Furthermore, cultures of each of the lines were compared periodically with photographs and descriptions of the same lines made in 1928 and the agreement always was very close, the appearance of the colonies often being identical with that in the photographs. The senior writer, who isolated the lines originally and studied them closely, never had the slightest difficulty in picking cultures of these lines out of a random assortment of cultures of many different lines.

The characters of colonies of the three lines on potato dextrose agar as recorded September 1, 1929, are given in Table 1.

In September, 1932, the color of A8-3-1 still was distinctly grayish olive and yellowish white, that of A8-5-5 was orange buff, and that of A8-5-3-3-2 was white, with a tinge of purplish brown near the center. There never would have been any difficulty in distinguishing the lines from each other by color alone. The characteristic elevation, luster, surface and topography, and edge of colonies of the same line also were so persistent as to justify the conclusion that these characters are due to genetic factors. If the colonies in the 1929 and 1932 series on potato dextrose agar are compared carefully, it will be seen that they are very similar in essential characters, although the expression of the characters differs somewhat for the reasons already mentioned (Plate 28). On potato malt agar growth usually is more rapid than on potato dextrose agar, colonies become larger and coarser, but the color is about the same and the other characters are of the same general nature as on potato dextrose agar. That the characters of the colonies are due to the interaction of genetic and environmental factors is obvious; in fact the elementary principle on which this statement is based is illustrated beautifully by the behavior of these lines of *U. zaeae*.

⁴ Minn. Tech. Bul. 65. 1929.

TABLE 1

Cultural characters of three lines of W. Va. A8 derivatives growing on potato dextrose agar. Taken from Minnesota Technical Bulletin 65, Table IV, p. 17.

LINE	DIAM. IN MM.	COLOR	ELEVATION	LUSTER	SURFACE AND TOPOGRAPHY	EDGE
A-8-3-1	56	Gray drab on central knob; surrounded successively by olive drab, gray drab, and dirty yellowish-white zones	Convex-umbonate	Dull to cretaceous	Central area rugulose; surrounded by coarsely rugose zone, and broad marginal zone almost flat; radial folds extending 1 centimeter from central area but not reaching margin	Fimbriate
A8-5-5	55	Orange buff	Convex	Dull	Contoured; regular radial furrows in marginal zone	Entire
A-8-5-3-3-2	50	White; faint purple brown near center	Convex	Cretaceous	Verrucose	Slightly fimbriate

There is additional circumstantial evidence from study of these lines that sectoring often is due to mutation rather than segregation. Some, notably A8-7, A8-8, A8-9, and A8-10, never had produced sectors from the time they were isolated in February, 1928, until November, 1931. Then sectors appeared in A8-9 and A8-10, after which A8-10, particularly, showed a tendency to sector occasionally. One of the new lines, A8-10-1, is shown in Plate 27 above its parent, A8-10. It seems improbable that segregation would be delayed for almost three years. Furthermore, A8-3-1, which appeared as a sector in a culture of A8-3 in June, 1928, was kept under close observation because of its very characteristic appearance, and it never produced sectors until September, 1932, when several appeared. One of them was especially distinct and was studied carefully. The basic color of the parent, A8-3-1, was light grayish olive, while that of the variant, A8-3-1-1, was almost ivory white; aerial growth was fairly abundant on colonies of the parent, while there was very little on those of the variant; the parent line produces a light vinaceous color in the medium, while the new line does not discolor the medium. The new line therefore appears to have lost factors for aerial growth and pigmentation of the medium. Here again it seems unlikely that segregation would have been delayed more than four years. The appearance of the two lines is shown in Plate 27.

The above facts support statements made by Stakman, Christensen, Eide, and Peturson³ (p. 50) to the effect that "mutant" lines of *U. zeaе* may be quite variable phenotypically but are genotypically distinct and constant except as they may change by "mutation."

Experiments also were made to ascertain whether the pathogenicity of the variant lines had remained constant. All of the lines are unisexual; consequently normal infection and production of chlamydospores do not result when corn is inoculated with a single line. Therefore, the only method of determining pathogenicity is by inoculating with combinations of lines of different sex. In the winter of 1928-29 Golden Bantam sweet corn had been inoculated hypodermically with W. Va. A8 and some of its derivatives in combination with Minn. A and Italy A1. In the late fall of 1932 Northwestern Dent corn was inoculated with the same combinations, as shown in Table 2. The methods used were similar to those previously described by Stakman and Christensen.⁵ The notes on the two series inoculated several weeks apart in 1932 were taken without reference to the results obtained in 1928-29. Furthermore, the pots inoculated with the different combinations were designated by key numbers in order to avoid personal bias in recording the degree of infection. When the results were compared with those obtained almost four years previously, it was found that there was surprising agreement, all the more remarkable and noteworthy because different varieties of corn had been inoculated.

The results (Table 2) show clearly that the pathogenicity of the lines had not changed, the degree of infection caused by particular combinations of lines being very uniform throughout.

In 1928-29 all of the lines, except W. Va. A8-5-3-3-2, which caused no infection either with Minn. A or Italy A1, caused heavier infection in combination with Minn. A than with Italy A1. This was true also in 1932. W. Va. A8-1-1 so consistently produced heavier infection than its original ancestor, W. Va. A8, both with Minn. A and Italy A1, that it appears to have gained factors for sex or pathogenicity, or both, or to have lost inhibiting factors. W. Va. A8-5-5 and W. Va. A8-5-3-3-2 clearly are less virulent in both combinations than the original ancestral line, W. Va. A8. Apparently both are devoid of certain factors possessed by the other two W. Va. lines.

It is evident that different combinations of lines may differ in virulence. And it is clear also that these differences must be due to genetic factors; otherwise they could scarcely be so consistent. W. Va. A8-1-1 x Minn. A was the most virulent combination in 1928-29 and again in 1932. W. Va. A8 x

⁵ Stakman, E. C., and J. J. Christensen. Heterothallism in *Ustilago zeaе*. *Phytopath.* 17: 827-834. 1927.

TABLE 2

Results of inoculating Golden Bantam corn hypodermically with combinations between certain monosporidial lines of Ustilago zeae in 1928-29 and Northwestern Dent corn with the same lines in 1932.

LINES	MINNESOTA A			ITALY A1		
	1928-29	1932		1928-29	1932	
		SERIES 1	SERIES 2		SERIES 1	SERIES 2
W. Va. A8	$\frac{11}{12}$ M+	$\frac{12}{18}$ M+ to I	$\frac{9}{18}$ M+	$\frac{9}{11}$ I to S+	$\frac{10}{16}$ I to M	$\frac{9}{18}$ I to S
W. Va. A8-1-1	$\frac{10}{10}$ M++	$\frac{14}{15}$ M+	$\frac{16}{20}$ M++	$\frac{8}{10}$ M+	$\frac{10}{11}$ M+	$\frac{11}{17}$ M+
W. Va. A8-5-5	$\frac{7}{11}$ I to S-	$\frac{7}{17}$ I	$\frac{7}{18}$ I to S	$\frac{0}{11}$	$\frac{1}{20}$ I	$\frac{3}{20}$ I ^a
W. Va. A8-5-3-3-2	$\frac{0}{15}$	$\frac{0}{19}$	$\frac{0}{22}$	$\frac{0}{11}$	$\frac{0}{19}$	$\frac{1}{22}$ ^b

* = no spores; ^b = probably accidental

The lines crossed with Minn. A and Italy A1 are listed in the vertical column on the left in the table. The results are expressed in the form of a fraction, the denominator indicating the number of plants inoculated and the numerator the number that became infected. Inoculations also were made with each line singly, but no infection resulted, showing that all are uni-sexual.

The degree of infection is indicated as follows:

- I Indicates incipient infection, that is, decided chlorosis and sometimes slight swellings; usually, however, without the production of chlamydospores
- S indicates small galls
- M indicates medium size galls
- + and - after letters indicate fluctuations within the class. M++, for example, means galls which are near the upper limit of medium size; S- means that the galls were very small. The first letter indicates the predominant type of infection.

Minn. A and W. Va. A8-1-1 x Italy A1 probably do not differ appreciably from each other, as both caused the same degree of infection in 1928-29 and 1932. W. Va. A8-5-5 x Minn. A caused only very weak infection in all three series of inoculations, the degree of infection being virtually the same each time. W. Va. A8-5-5 x Italy A1 caused no infection in 1928-29, and produced only a few very minute galls in 1932, without producing chlamydospores, however. This very slight difference may be due to normal variability, or Northwestern Dent corn may be slightly more susceptible to this combination than Golden Bantam.

Not only did the W. Va. lines remain constant in pathogenicity, but Minn. A and Italy A1 must also have remained constant, since they entered into the dikaryotic combinations which produced the same degree of infection at the different times. It is clear that there was no appreciable diminution in virulence of any of the lines as a result of having been grown for nearly four years on artificial media subsequent to the time the first inoculations were made.

The results of the inoculations strengthen the conviction that, in the case of *U. zeaе*, new lines arising by sectoring in cultures are the result of genotypic changes, which sometimes involve factors for sex and pathogenicity as well as cultural characters. This supports the conclusions previously reached in the study of constancy of cultural characters. Furthermore, the fact that none of the variants was of entirely different sex from the original line suggests that they arose through mutation rather than delayed segregation.

SUMMARY

1. From a single monosporidial, unisexual line of *Ustilago zeaе*, W. Va. A8, 162 distinct lines arose in 1928 as sectors in colonies of the original line and its variant derivatives.

2. Fourteen variant lines have been cultured on artificial media from early in 1928 until the present time. While they are variable phenotypically, distinctive cultural characters have persisted so definitely as to justify the conclusion that each of the lines constitutes a distinct biotype, from which new biotypes may, however, arise by sectoring.

3. Some of the variant lines produced no sectors for about three years, when several distinct ones appeared, from which new lines were isolated. This supports the idea that sectoring results from mutation rather than delayed segregation, although delayed segregation may sometimes occur.

4. The pathogenicity of the original line, W. Va. A8, and several of its derivatives was tested early in 1928, by mating them with Minnesota A and Italy A1. It was evident that some variants differed from A8 and each other in factors for sex and pathogenicity, although none of the variants combined with the original line and each other, indicating that there had not been a complete change of sex. This suggests that they arose through mutation rather than segregation. Late in 1932 inoculations were made with the same combinations of lines, and the results were almost identical with those obtained almost four years previously. This again indicates that the variant lines resulted from genotypic changes and are new biotypes.

5. It is evident that a large number of biotypes may arise from a single unisexual, monosporidial line, by what appears to be mutation. They may

differ from each other not only in factors for cultural characters but also for sex and pathogenicity.

6. Since the pathogenicity of individual biotypes derived from a single monosporidial line may differ, it is evident that chlamydospore collections or so-called physiologic forms of smut fungi may comprise a very large number of biotypes.

UNIVERSITY OF MINNESOTA

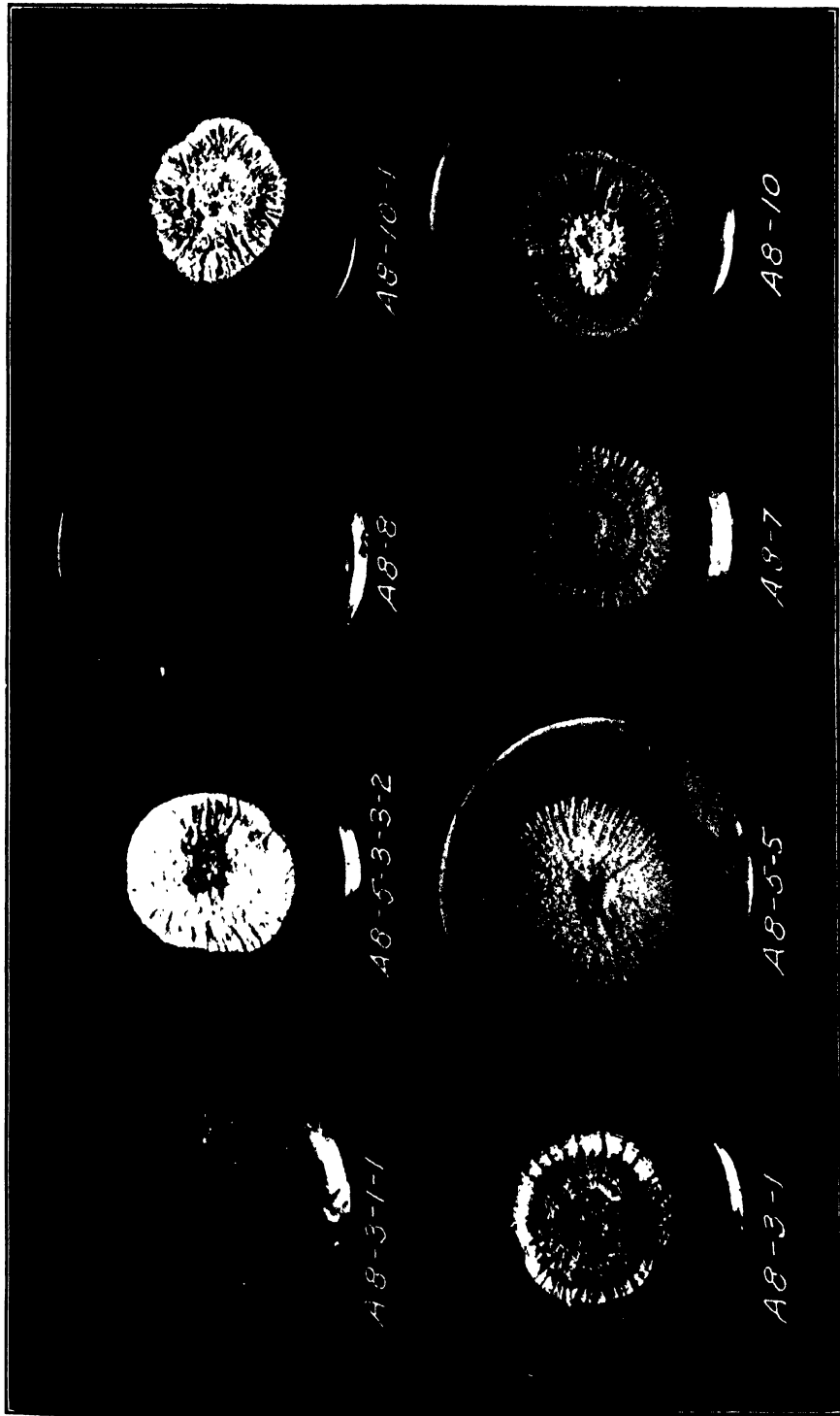
Explanation of plates

Plate 27

Eight variant derivatives of W. Va. A8. All have retained their distinctive cultural characters for 4½ or 5 years, except A8-10-1 and A8-3-1-1, which arose fairly recently as sectors in A8-10 and A8-3-1-1, respectively.

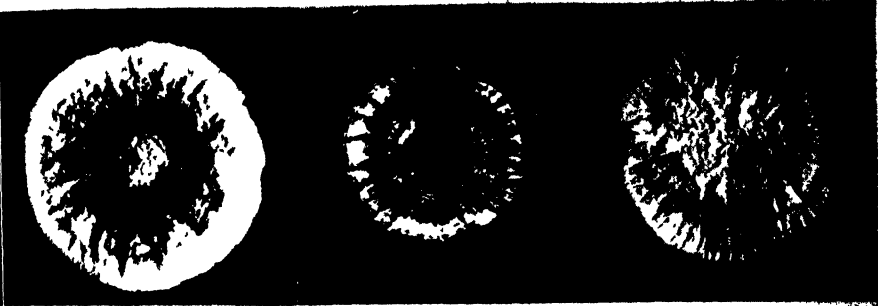
Plate 28

Three variant lines of the W. Va. A8 series. Left, colonies of the 3 lines on potato dextrose agar in 1929; middle, the same 3 lines on potato dextrose agar in 1932; right, on potato malt agar in 1932. This shows phenotypic variability but indicates genotypic stability, as the distinctive characters of each line are persistent.



STAKMAN, TYLER AND HAFSTAD USTILAGO

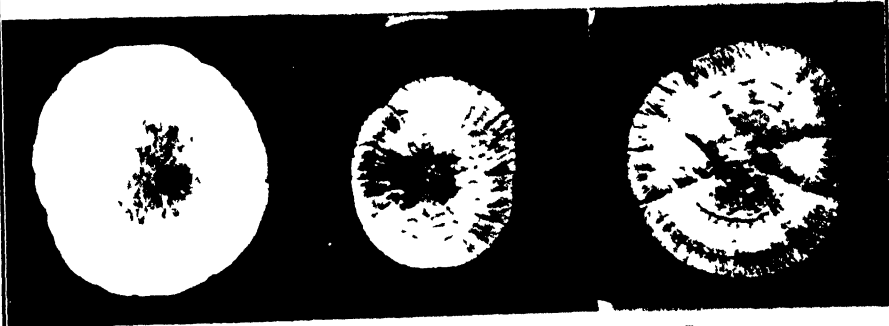
Ustilago zeae



W. Va. A8-3-1



W. Va. A8-5-5



W. Va. A8-5-3-3-2

1929

1932

PDA

PDA

PMA

The germination and growth of *Peltandra virginica* in the absence of oxygen¹

THOMAS I. EDWARDS

(WITH TWO TEXT FIGURES)

Germination in the virtual absence of oxygen has been reported for *Alisma Plantago* by Crocker and Davis (1914) and by Schaumann (1926). The anaerobic germination of rice has been observed by a number of workers, including Nagai (1916) and Sasaki (1930). Similar reports have been made for the seeds of *Typha latifolia* and *Cynodon dactylon* by Morinaga (1926); for *Nelumbo nucifera* seeds by Ohga (1926), for *Trapa natans* by Teresawa (1927), and for *Euryale ferox* by Okada (1930). It is worth noting that all of these plants grow in, or close to, water, and that all but *Trapa natans* are monocotyledonous plants. Several methods have been used by these workers for removing oxygen from their cultures. These include displacement of air by an inert gas, usually nitrogen or hydrogen; absorption of oxygen in alkaline pyrogallol; and removal of atmospheric oxygen by the use of a suction pump. The last method provides the severest test because it removes the air from the spaces between the seed organs and to some extent from the intercellular spaces also.

In addition to these papers there are numerous reports of failures to secure germination of the seeds of the common crop plants in atmospheres of very low oxygen tension. These began to appear soon after the discovery of the air pump. Also, soon after the discovery of the commoner gases experimenters tested their effect on germination without finding any seeds that were capable of germination in the absence of oxygen. The only other group of papers requiring to be mentioned here is that reporting efforts to grow plants in rarified atmospheres. Representative of this type of work are the papers of Wieler (1883) and Nabokitch (1903). Their objective was to measure the elongation of plant organs of cultivated species at exceedingly low oxygen tensions. The weakness of these experiments is to be found in their failure to discriminate between mere elongation (the physical phenomenon of taking in water and expanding pre-formed cells) and growth in the stricter sense (including division of cells in a meristematic region, elongation, and maturation).

The present paper deals with the ability of the seeds of *Peltandra virginica* (L.) Kunth., a member of the Araceae, to germinate in an atmosphere nearly, if not completely lacking oxygen, and to elongate their plumules from two to three times their original length under these conditions.

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MATERIAL

The seeds of *Peltandra virginica* used in this study were collected from plants growing on a muddy bank or in shallow water just above the Great Falls of the Potomac River on the Maryland shore in October, 1932. This species grows in marshes throughout the eastern part of the United States. Its seeds are imbedded in a tenacious jelly and are surrounded by a tough pericarp. The seeds, which weigh about 0.8 gram each, on the average, consist of a large, well-developed and slightly curved embryo whose plumule is about 8 mm. long, lying in a groove along a large mass of starchy endosperm. The seeds needed only to be removed from the pericarp to be capable of germination and any injury to the pericarp or the attack of a fungus was enough to initiate germination. At the time of collection the seeds germinated slowly but after several months storage in the fruit coats at room temperature, and also in seeds freed from the coats and stored at 5°-8°, germination occurred in much less time. Usually the plumule was the first part of the embryo to emerge from the seed.

NUMBERS OF SEEDS PER FRUIT

Of 757 *Peltandra virginica* fruits examined, 719 contained only one seed, 34 two seeds, and 4 fruits contained three seeds. When plotted these data give rise to a so-called J-shaped distribution which falls off very steeply. The biometric constants for this distribution and their probable errors are as follows: average number of seeds per fruit $1.055 \pm .006$; standard deviation $.251 \pm .004$; coefficient of variation $23.8 \pm .4$. When more than one seed was found in a fruit the seeds were usually of about the same size but somewhat smaller than the seeds which occupied a whole fruit and were flattened where they touched each other. Only seeds from single-seeded fruits were used for these experiments although the others germinated in satisfactory manner.

Counts of this kind have been reported for the fruits of a number of species which reveal some differences in frequency distributions. For the bilocular and trilocular fruits of *Ptelea trifoliata* Harris (1911a) found distributions much like that of *Peltandra*. According to the same author (1912) *Crinum longifolium* and also (1911b) *Staphylea trifolia* and *Cladastris tinctoria* have larger numbers of seeds per fruit than *Peltandra* but they too bear one-seeded fruits more frequently than any other kind and their distributions of seed number may be represented by curves of this sort. In these sets of data Harris recorded the presence of small numbers of fruits containing no seeds and when this was represented graphically the curves became strongly skewed. No records were taken of the possible occurrence of such fruits in *Peltandra*.

More frequently, however, curves approaching the form of the normal Gaussian curve have been obtained. Pearson (1901) reported the seed frequencies of *Cytisus scoparius*, *Lotus corniculatus*, *Lathyrus odoratus*, *L. sylvestris*, *Vicia Faba*, and *V. hirsuta*, all but *Lotus* having fairly symmetrical distributions. Pearl (1906) described the numbers of seeds found in a collection of *Nelumbium luteum* fruits and calculated the descriptive constants of the distribution. Harris (1909) confirmed Pearson's findings for *Cytisus* and later (4) studied the distributions of *Sanguinaria canadensis* seeds in collections of fruits made in two seasons. Harris's (1916) data for *Cercis canadensis* fall on a very symmetrical curve. In most of these cases the mean number of seeds and the standard deviations are much greater than for *Peltandra* but the coefficients of variation, which show the relation of the standard deviation to the mean, are roughly of the same magnitude.

It is conceivable that many factors may influence the numbers of seeds that may ripen in the fruits of a given species, important among them being the number of ovules laid down during the development of the flower and the number of these that are fertilized. The seed counts made on *Peltandra* fruits are based on the number of seeds that reach maturity but probably many others attain only a fraction of their development. In these counts there has been no attempt to record the number of seeds that reached, for instance, only a fourth of their development before being crowded out or robbed of food by more vigorous seeds. If it were possible to estimate these partial stages of development in a quantitative manner it would be necessary to deal with fractional values in studying seed distributions, and the frequency curve would have to show classes between zero and one seed per fruit. In such a case the appearance of a J-shaped curve would be lost and instead one would have an extremely skewed frequency curve. There does not seem to be any reason at present for regarding these asymmetrical distribution curves as being radically different in kind from the nearly symmetrical distributions. It would seem that any attempt to interpret the biological significance of these curves must rest upon a closer study of the living plant throughout the growing season in order to note at what stages the development of individual ovules is arrested and to ascertain the causes of these failures. At present it is not possible to carry this study further on *Peltandra*. It is worth noting, however, that this tendency toward the production of one-seeded fruits does not seem to put the species at any conspicuous disadvantage to judge from the relatively wide geographical distribution it has on this continent. It is found growing in marshes as far south as Florida and Louisiana and as far north as Maine and Michigan.

METHODS

In order to decide upon a suitable temperature for carrying on these tests, measurements of the growth of 6 *Pellandra* seedlings in darkness were made at each of 6 constant temperatures. The seeds were laid on moist sand in tall, rectangular, glass jars which were kept covered. Growth was most rapid at 29° with the 25° cultures not far behind. The 35° seedlings were quite irregular in size, the best of them growing slightly slower than the 25° ones. At 20° growth was slower still; at 15° it was greatly delayed, and at 12° plumules did not develop during the month the cultures were kept under observation, although subsequently some growth did occur. A large number of seeds freed from the pericarps were stored at 5°–7° and in the course of six months many of them germinated and the plumules elongated a few millimeters. These seedlings lacked the normal geotropic response.

Soon after the seeds were collected preliminary tests showed that they were able to germinate and the plumules were capable of elongation if the seeds were submerged in water through which hydrogen from a simple generator was bubbled, and also when they were exposed over alkaline pyrogallol. The tests which best indicate their ability to germinate and to grow in exceedingly low oxygen tensions were made six months later after the seeds had been stored at 5°–7° in darkness, conditions under which germination goes on very slowly. Three *Pellandra* seeds were introduced into each of a number of soft glass vials, 2.5 cm. in diameter and about 15 cm. long. By manipulation in a flame a zone of glass about 11 cm. from the bottom was allowed to soften and to form a thick-walled tube, 1–2 mm. in diameter, the seeds being kept cool during this process. When the tube had cooled about 10 cc. of tap water were introduced into the part of the tube containing the seeds, the tube was connected to a water aspirator and the atmospheric pressure reduced until the water boiled at room temperature (about 23°C.). The evaporation of the water was often hastened by heating to about 30°. This procedure undoubtedly had the effect of washing out all but traces of the atmospheric gases left in the tube, to say the least, and also of removing the gases from the intercellular spaces of the seed. When nearly all of the water had been evaporated the tube was sealed off in a small flame without any interruption to the suction and as soon as the glass had cooled the culture tube was entirely submerged in water strongly colored with dye so that if any leakage occurred it would be evident on inspection of the seeds. Tubes so sealed, together with controls consisting of seeds in open tubes, were cultured in darkness at 24°, a temperature a little below the optimal temperature for growth, and after growth had ceased they were removed, measured, and photographed.

It should be noted that three factors contribute toward reducing the oxygen tension. (1). At the very first operation, gaseous pressure in the tube was reduced to about 20 mm. Hg, which removed the greater part of the oxygen originally present. (2). Approximately 10 cc. of water is evaporated at this pressure, which theoretically should occupy a volume of more than 500 liters when reduced to vapor at 23° and 20 mm. Hg, and the continued production of water vapor during suction would displace all but traces of oxygen from the culture tube. (3). The respiratory activity of the seeds themselves would be expected to use up oxygen, and since the cultures were in darkness no additions of oxygen as a result of photosynthesis could occur. If any gaseous oxygen can remain after this treatment its concentration must be exceedingly small.

RESULTS

Figure 1 is a photograph of treated seedlings and controls taken 9 days after the tube at the left had been sealed off in the manner just described. It is typical of five other experiments in which *Pellandra* seeds were sealed in tubes of this and other forms and into which no leakage occurred. This particular experiment was started with seeds whose plumules had just begun to elongate and in the almost complete absence of oxygen they grew to lengths of 3.0, 2.2, and 2.2 cm., or until in the presence of air the first foliage leaf would have broken through the coleoptile. Instead, however, no further development of the plumule occurred; the control seedlings in the tube at the right developed two foliage leaves in the same time and under the same conditions. Root development was almost completely suppressed in the absence of oxygen although it was vigorous in the control seedlings.

Even though *Pellandra* seedlings are cultured in darkness and are examined at infrequent intervals only in weak light the seedlings are greenish, even more so than the controls. Microscopic examination of the seeds stored at low temperature in darkness for six months shows an abundance of green chloroplastids throughout the embryonic plumule and in the first three layers of the endosperm. It appears that these merely persist in the seedlings grown in darkness, and that there is no reason to assume that chlorophyll formation takes place under these conditions. If this is so then the deeper green of the seedlings cultured anaerobically might be due to the circumstance that the surface area is smaller and the plastids are more concentrated on that account.

When the culture flasks were broken open at the end of an experiment there was no trace of any odor which might have been attributed to putrefaction; the seedlings normally have a peculiar but not unpleasant odor

when they are grown in air and nothing but this was apparent in the sealed tubes. The tips of other tubes were broken under dilute NaOH solution; at first the liquid filled about $1/3$ of the tube, but in a short time almost all

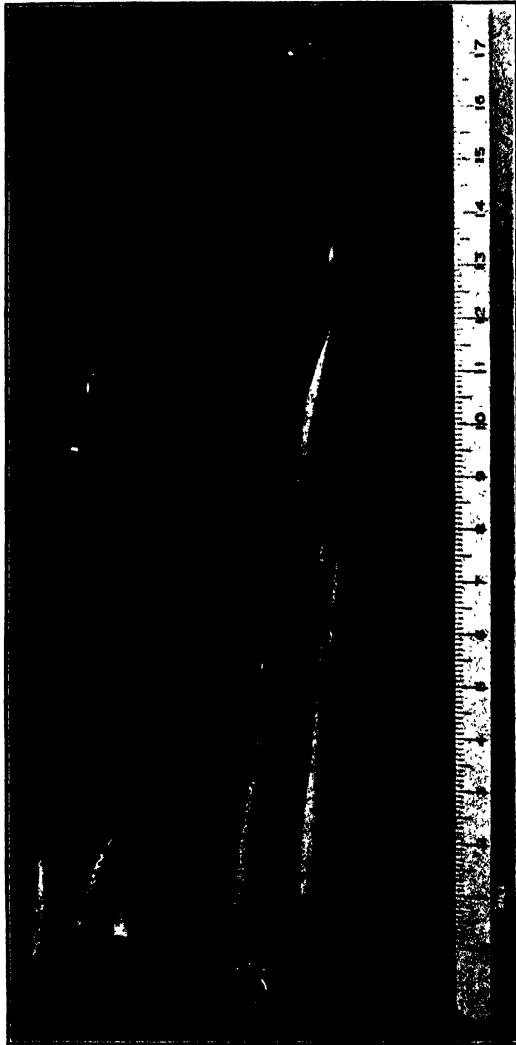


Fig. 1. *Pellandra virginica* seedlings nine days old. The ones at the left grew in the absence of oxygen; the controls at the right were grown in air.

of the gas was absorbed. This gives a rough indication of the high carbon dioxide tension prevailing in the sealed culture tubes. The small amount of gas remaining was not soluble in alkaline pyrogallol and as a gas analysis apparatus was not available its nature is unknown.

Seedlings which had ceased to grow under anaerobic conditions were fixed, sectioned, and stained for a comparison of their tissues with those of seed embryos and to permit an estimate of the likelihood of cell division under anaerobic conditions. The photomicrographs of Figure 2 were prepared from such sections and show the appearance of portions of the coleoptile and the first foliage leaf. The upper photograph is a median longitudinal section through a seed which had not begun to elongate and shows

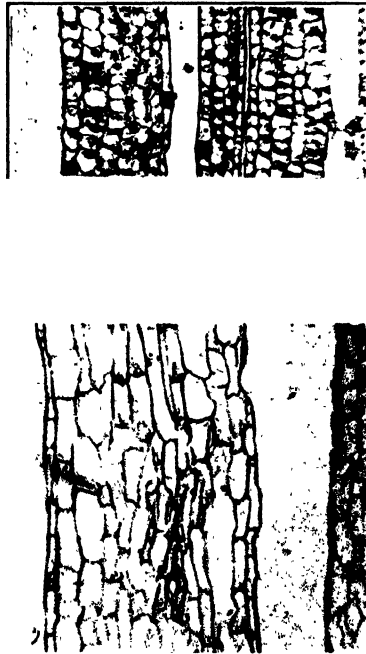


Fig. 2. Photomicrographs showing median longitudinal sections through the coleoptile and adjacent leaves of *Peltandra virginica*. Above, through the seed embryo. Below, through a seedling which had ceased to grow in the absence of oxygen. 56 \times .

cells that are approximately square. In the lower photograph prepared from a comparable section through one of the seedlings shown in Figure 1, and taken at the same magnification, the cells appear to be 2-4 times as long as they are broad. This section passes close to a vascular bundle. Since the cells elongate to these proportions, and since the whole organ increases in length only 2-3 times there would seem to be no need to suppose that any new cells were formed in order to account for the observed elongation, especially since there was only a slight increase in the thickness of the coleoptile. Moreover, in the coleoptile as it was observed in the seed there are no cells that have the appearance of meristematic tissue when com-

pared with the stem growing point. From these observations it would appear that the increase in length of the seedlings was due to the elongation of cells already formed in the embryo.

Three other kinds of seeds were tested in the same way as the *Peltandra* seeds, viz. rice, cress, and sunflower, the latter two failing to germinate. The longest rice coleoptile was 2 cm. in length and several others were nearly as long. Like the rice seeds cultured by Nagai (12) in the absence of oxygen, these rice seedlings did not develop roots. On the whole, the performance of rice seeds was essentially the same as that of *Peltandra*.

DISCUSSION

Perhaps the most striking feature of these experiments is the evidence they present of the unusual tolerance these plants must possess to the products of their own anaerobic respiration. Almost all plants so far studied have been able to carry on respiration for a time in the absence of oxygen, but it appears that they poison themselves with the accumulation of metabolic products which in the presence of oxygen are oxidized to relatively inactive substances, usually carbon dioxide and water. Either these *Peltandra* seedlings possess a type of respiratory metabolism that produces non-toxic intermediary products when complete oxidation is prevented, or if their metabolism is not greatly different from that of most other plants so far studied their tolerance to these metabolic products is far higher. There are not enough seeds of this lot left to permit an extensive study of this question at the present time.

It is a pleasure to acknowledge the advice and assistance of Professor Raymond Pearl during the preparation of this paper.

SUMMARY

The seeds of *Peltandra virginica* are able to germinate in the almost complete absence of oxygen and under these conditions the coleoptile may elongate two or three times its original length. This seems to be due entirely to the elongation of cells already formed in the embryo. Rice also germinates and develops to about the same stage as *Peltandra*; cress and sunflower do not.

Of 757 *Peltandra* fruits examined, 719 were one-seeded, 34 two-seeded, and 4 contained three seeds.

Preliminary tests showed the optimal temperature for seedling growth in air to be about 29°C.

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On the vaccination of the tobacco plant against *Thielaviopsis basicola*

CARLO ARNAUDI¹

(WITH FOUR TEXT FIGURES)

Until a few years ago, vegetable immunology was essentially natural immunology, and the study of natural susceptibility and resistance to disease held the field. The differences in resistance of certain species to given diseases were considered to be due only to environmental conditions, such as climate and nutrition, or to inherited characteristics.

It was shown some thirty years ago by Beauverie (1901) that plants could acquire active immunity by a process analogous to that of vaccination in animals, and in the same year other and equally positive tests were reported by Ray (1901). This line of work, however, was not followed up for more than twenty years, except by Bernard (1911), Magrou (1921) and Hiltner and Stoermer (1923), and they were concerned with resistance to super-infection rather than vaccination.

The then current ideas on the pathogenesis of plant diseases did not recognize the probability of the occurrence of immunological reactions of the animal type in the vegetable organism. On the contrary, the theories used to explain the phenomena of animal immunology emphasized those humoral reactions which one can hardly think of in connection with plants, and took too little into account the cellular defense which is evident even in plants. Thus an obstacle arose to the institution of parallels between the two kingdoms, particularly for those botanists who kept in view those organismic and autonomic cellular characteristics of plants that undoubtedly are among those most sharply separating plants from animals.²

This mental attitude of the vast majority of phytopathologists not only created conditions unfavorable to the development of modern immunological ideas, but led the research workers to overlook those cases of

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² It is curious to note how almost as if to substantiate their opinions, some of those workers who denied the possibility of vaccinating plants, granted to animal vaccination a range which it actually does not possess. In fact, the number of infectious diseases in animals and in man in which vaccine therapy is clearly efficacious is not great. Even in the few most favorable cases 100% of success is never obtained. Effective vaccination is extremely variable and often of brief duration, and direct relations between circulating antibodies and immunity rarely exist. Nevertheless, the service that vaccine therapy has rendered and still renders in the struggle against infectious diseases in man and beast, is of the highest importance, and its introduction constitutes one of the greatest conquests of modern medicine.

naturally increased resistance in plants or their organs which might have been explained as cases of natural vaccination. Consequently, many individual phytopathological phenomena were disregarded which, had they been collected, studied, and compared, might have increased our knowledge of the genesis of plant diseases. Montemartini (1931) has recently examined both old and new works written with purposes and concepts far removed from those of our studies and has drawn from them deductions of the greatest interest.

The question of acquired immunity in plants was again taken up by Carbone (1919), who in a series of critical studies placed the problem of plant immunity in the picture of general immunity. He distinguished and marked the limits of the tasks of the two fundamental groups of research workers in our field: those who study the active artificial immunization of plants, and those more strictly theoretical investigators who study the production of vegetable antibodies and their presence in the cellular and circulating juices.

Next we have the notable experimental contribution by Zoja (1924), who immunized wheat against *Helminthosporium sativum*. Arnaudi (1925), in turn, vaccinated potato tubers against a *Bacillus* of the *B. mesentericus* group. And Hursh (1925) showed that a treatment of the stalks and leaves of wheat, cabbage, cauliflower and other plants with sterile filtrates of *Leptosperia herpotrichoides*, *Fusarium vasinfectum* and *F. oxysporium* fortified them against a second and more powerful treatment with the same filtrates.

In 1926 appeared the report of the researches by Sieden and Trieschmann, who immunized potato tubers against "cancer," and in 1927 that by Benigni who immunized small maize plants against *Ustilago Maidis*. Arnaudi in 1928 again returned to this subject. By vaccinating small pea plants against *Blepharospora cambivora*, he demonstrated the specificity of the vaccination by treatment and cross-infection with other micro-organisms. In the same year Nobecourt reported vaccination of beans against *Botrytis cinerea* and *B. carotovorus*.

In 1930, Carbone and Arnaudi collected in a single monograph all that had been done in the field of acquired immunology in plants and coordinated the experimental facts which had been ascertained up to that time both by themselves and by other workers. They also elaborated a plan for future research.

In the following years, besides a noteworthy group of studies on plant antibodies by Kostoff (1929), Silberschmidt (1931) and Chester (1932) a few experimental contributions in the field of vaccination served to clear up certain details of its mechanism. Jarach (1932) discussed the proposi-

tion, put forward by some, that the plants supposed to be vaccinated were really rendered unsuitable for the development of the infectious organisms by impregnation with microbicidal substances in the vaccinating liquid.³ Working on the couple, dwarf bean and Toile [*Botrytis cinerea*], he showed that the phenomenon was due to reaction by the plant to the effect of the vaccine. Using a technique that does not alter the vaccine, he found that the pathogenic micro-organisms grew perfectly on a plant first vaccinated and then killed. Carbone and Kalaiew (1932) have continued the work on the mechanism of vaccination and have shown that the vaccine can not be precipitated by alcohol and that there is no parallel between the toxicity and the immunizing power of a vaccine. Using various chemicals and physical agents, they also produced degrees of injury in order to discover whether any particular state induced a higher degree of resistance to the pathogenic agent. They concluded that the vaccine exerted a specific action upon the protoplasm of the affected cells.⁴

At about the same time Leemann (1932) published his notes upon the natural influence of pathogenic or non-pathogenic micro-organisms of the soil on the receptivity and resistance of plants; he also described his experiments on the immunization of wheat against *Helminthosporium sativum*.

A few workers, in the meantime, invoked naturally acquired active immunity to explain cases of greater resistance, which certain plants showed against various parasites. Montemartini (1930) supposed that the progressively increased resistance to *Oidium*, which is shown by the oak, is due to slow natural immunization, and he supports this view with experimental evidence. East (1931) came to an analogous conclusion in the case of the mosaic disease of the sugar cane. East (1930-31) also placed in high relief the possibility of an important connection between the views of modern vegetable immunology and experimental genetics. According to him, those varieties of sugar cane that show greater resistance to the mosaic disease have undergone a progressive process of vaccination, which is recognizable by precipitation reactions on the juices. The plants that had

³ This phenomenon has been described repeatedly with experimental evidence. Potter (1909) described an experiment in which he inoculated the culture-liquid filtrate of a *Penicillium* into the fruit of the orange; he noted that the *Penicillium* no longer grew in these fruits while it continued to develop on other untreated ones. He supposed that the metabolic products of the fungus protected the plant, but it is not impossible that even in this case actual immunization took place.

⁴ In connection with the mechanism of vaccination, I may mention some unpublished experiments of my own upon the bean, using the Toile as the agent. I wished to note the effect of repeated vaccinations, using constant or variable quantities of vaccine. The results were uniformly unfavorable. In fact, there was sometimes a slightly higher degree of sensitiveness in the plants treated than in the controls.

overcome the disease react to the precipitation test like those that, apparently healthy, acted as carriers, while those which have never suffered from the disease in any degree differ profoundly in their reaction to the test.

The most recent contribution to our problem is that of Gheorghiu (1932), who has introduced into vegetable vaccine therapy the concept of local immunity and using a technique inspired by that idea and vaccinated plants of *Pelargonium* against *Bacterium tumefaciens*. Arnaudi (1928) had already demonstrated the resistance to superinfection by *B. tumefaciens* shown by *Pelargonium* having tumours, when the new inoculation is made rather close to the primitive tumour. Now Gheorghiu so planned his experiments as to bring out the local action of the vaccine, and the corresponding cellular reaction of the tissues showed that increased resistance to the primary infection could be obtained.

In the works here briefly summarized, we have confirmation of the conclusions, reached by Carbone and Arnaudi in their monograph, that the natural resistance of phanerogams to the infectious action of cryptogams⁵ may be increased when the former have undergone and overcome a first attack of the disease, or when they have absorbed killed germs or materials derived from the infectious germs themselves.

In the works mentioned above the operative treatment has been given in detail in order to emphasize the conditions which are most favorable for the observation of increased resistance to parasites and for the study of the mechanics of the reactions. These investigations have been exclusively theoretical in character. In the experiments described in this article a first attempt is made to vaccinate plants as an agricultural technique. We have not yet set up rules for a general application of vegetable vaccine therapy, but our laboratory experiments have been carried out with this in view.

In the monograph of Carbone and Arnaudi (1930) we foresaw practical applications of vegetable vaccine therapy as follows: (1) An indirect application through the experimental production of species and varieties in which natural resistance to parasites is reinforced.⁶ (2) A direct application by which valuable plants—particularly those which are raised from seed—are treated and then transplanted.

⁵ Heinricher (1929) has demonstrated that the pear increases its resistance to the mistletoe following a first attack by that parasite. This leads one to think that the phanerogams have a possibility of acquiring resistance to higher forms of parasites also.

⁶ The research work in this direction, being necessarily extremely laborious and calling for the use of a large number of plants, should be facilitated by the method of iarovisation devised by T. D. Lyssenko. This method allows the vegetative cycle of the plants to be shortened materially.

We therefore chose the tobacco plant as desirable material. Among the diseases of the tobacco plant, as an etiological agent that can be cultivated artificially—which is a fundamental condition if the preparation of the vaccine is to be easy, we chose *Thielaviopsis basicola*. It seemed to us that this agent was the most suitable for our purposes because of its wide diffusion in nature and because of the serious damages which it causes every year in tobacco plantations. On the other hand, *Thielaviopsis basicola*, as is well known, does not cause disease of an acute character, its toxic action being low; the infection manifests itself rather slowly; the attack

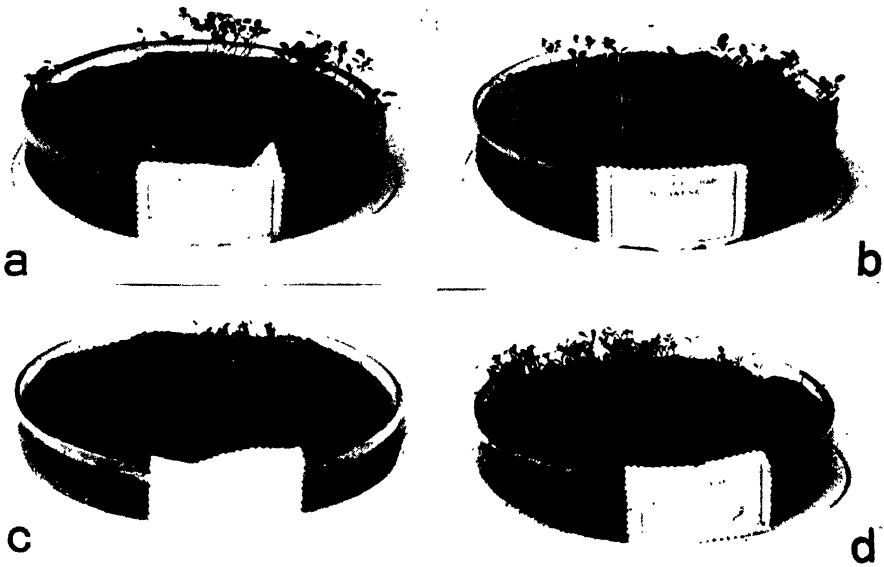


Fig. 1. Tobacco plants treated with *Thielaviopsis basicola* and *Pythium* vaccine. Note the various pathological symptoms caused by *Thielaviopsis* vaccine ether (c), *Thielaviopsis* vaccine heat (d), and *Pythium* vaccine heat (b), as compared with the control plants (a).

on the roots and the "collar" of the seedlings takes place without producing manifest symptoms of suffering. It is only when the infections continue that the plant becomes backward in development, so that at the ordinary time of transplantation, if the infection is great in the seed bed, it will be found that a lesion has developed which has cut off the stem from the root. These characteristics are such as to make experimental attempts at vaccination more difficult and to disturb estimates of the intensity of infection. For similar reasons the characteristics are not the most suitable for a study of the technique of preparation, administration, and effect of vaccinating materials. We were therefore forced to multiply the tests and to repeat the

same experiment many times in order to avoid erroneous interpretations of the results. Hence the research work was prolonged until the end of the summer of 1932. The entire experiments were carried out on the Berkley variety, with seed of 1930, which Dr. M. Donadoni, Director of the Angeloni Experimental Institute for Tobacco Culture at Scafati, was kind enough to furnish us and to whom I renew my sincere thanks.

The first vaccination tests were carried out with the technique and concept of the problem as a purely theoretical one, in order to collect the greatest possible number of observations from which to draw deductions applicable to practical work in vaccination. The tests were numerous, as I have already mentioned, but, for the sake of brevity, I will cite only a few of them here.

ORIENTATION TESTS

During the orientation tests lots of forty plants were used in each experiment. The seed was germinated in Petri dishes filled with sterile sand. When they showed the first signs of germination, small quantities of vaccinating material were poured on (about 2 cc. for each plate of 6 cm. in diameter). These tests were for the purpose of establishing the most suitable moment for administering the vaccine and for indicating to us the most favorable technique for preparation of the vaccine itself. Since the extreme delicacy of the plants makes it wise to disturb them as little as possible, the vaccinating material was administered as a fluid, in such a manner that it could be absorbed little by little into the sand and thus be carried to the root tips.

In all the vaccinations there was a first phase, immediately following application, during which the plants showed more or less intense signs of disturbance. These symptoms were of great variety and might be such specific traits as yellowing of the leaves, or browning of the root ends, or a more general symptom noticeable as retardation in development. These signs of suffering were not intimately correlated with intensity of the vaccine, as Carbone and Kalajev (1932) have shown, and as we shall show, later. One must regard the appearance of these signs as characteristic of the treatment and also, one might almost say, a proof of the activity of the vaccine material.

During these orientations four forms of vaccine were used, two based on cultures of *Thielaviopsis basicola*, and two based on cultures of *Pythium*. One vaccine in each pair was prepared by killing with ether, the other by killing with heat, in order to determine the conditions under which signs of disturbance in the tobacco plants were most evident.

These conditions were realized by administering the vaccinating liquid eight days after the seed had been planted (kept at 24°C.), that is to say,

at the moment at which the seeds were showing the maximum swelling or had commenced to sprout. The signs of suffering appeared after eight days and became more marked towards the twelfth day. The entire treated populations showed much more suffering than the controls, development in certain of the plants being only one-half of that exhibited by the controls (see figs. 1 and 2). Although the leaves did not show any particular characteristics of disease beyond a difference in degree of development and in number, the roots were more or less strongly tinged with brown, and in the lots treated with ether vaccine the epidermis showed lesions. In making a microscopic examination it was noticed that the epithelial tissues had become brown and slightly shrunken. These characteristics were com-

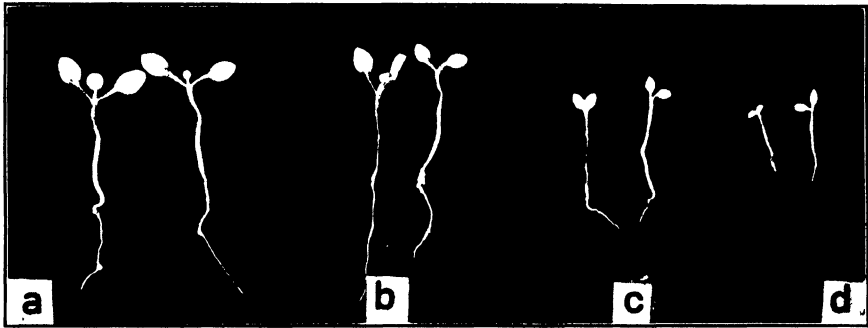


Fig. 2. Demonstration of the pathological symptoms caused by the various vaccines tested: (a) control; (b) *Pythium* vaccine; (c) *Thielaviopsis* vaccine (heat); (d) *Thielaviopsis* vaccine (ether). The photograph does not show the differences in color exhibited by the roots because it was taken on samples which had been kept in fixing liquid for some time, thus causing discoloration of the subjects.

mon to all the plants treated and appeared with greater intensity in the plants treated with ether vaccine of *Thielaviopsis basicola*, whereas they were extremely rare in the case of plants treated with *Pythium* vaccine, either of the ether-killed or of the heat-killed types (see fig. 2).

On the fifteenth day the plants were transplanted from the Petri dishes into ordinary flower pots containing sand. The manipulation was carried out by transferring small blocks of sand, in which the plants were fixed from the plates by means of a spatula, and depositing them cautiously in the prepared flower pots. Under these conditions the plants regained strength in a few days' time. Twenty days later their appearance was in no way different from that of the controls (see fig. 3 above). At this moment infection was produced by pouring into each flower pot a watery suspension extremely rich in *Thielaviopsis*. The flower pots were then transferred into the hothouse. The growth of the infecting agent was very weak,

probably owing to the fact that the earth in the flower pots was mixed with sand and constituted an unfavorable condition for the parasite. Clearly, a general infection was not obtained; nevertheless the results were positive. An examination made twenty days after the date of infection showed that while the general development of the plants was almost the same in all the lots, the number of the individuals was smaller in the controls and in the flower pots containing the plants treated with *Pythium*.

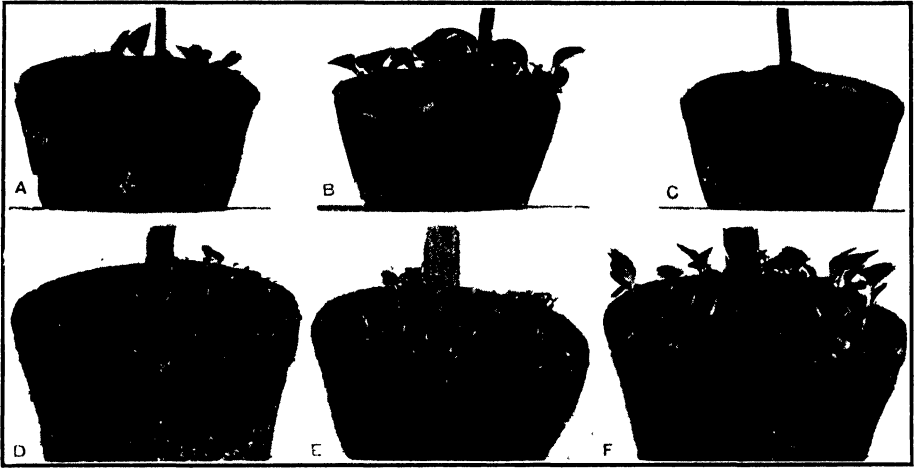


Fig. 3, above. The lots (a) heat *Thielaviopsis*-vaccine, (b) *Pythium*, and (c) control shown in figs. 1 and 2, thirty days after transplanting. Fig. 3, below. Lots of tobacco plants vaccinated with (e) ether *Thielaviopsis* vaccine, (f) heat *Thielaviopsis* vaccine at fourteen days after the experimental infection, as compared with (d) the control plants which were similarly infected.

SECOND SERIES OF EXPERIMENTS

During the second series of experiments the seeds were planted directly in the flower pots. At the first signs of germination, one group of pots was treated with the ether vaccine, a second with the heat vaccine, while a third group was kept as a control. The amount of vaccine used was 5 cc. of suspension for each pot of 10 cm. in diameter containing forty plants. At the moment of vaccination the drainage holes in the pots were closed, in order that the vaccinating material should not be carried away when the plants were watered. The pots were kept in the laboratory under a large glass bell jar, the better to regulate the temperature and the humidity. After ten days the first signs of suffering were observed. This time—besides the symptoms already noted in the orientation tests—it was found that the leaves were less green and were slightly smaller. These symptoms were particularly evident in the plants treated with ether vaccine. The plants

which were treated with the heat vaccine were only slightly less well developed than the control plants. Instead, the roots showed lesions similar to those already described. The seals were now removed from the drainage holes in the pots, and the plants were watered rather freely, in order to carry away the traces of the vaccines. Six days later, when all the plants had again acquired a similar and normal appearance, infection was made with a suspension of Thielaviopsis. To favor the growth of the infecting agent and to keep all the pots in a warm, humid environment, part of the plants were placed in the hothouse and part under glass bell jars in the laboratory. The plants were watered with a suspension of horse manure, decanted and filtered, to which 0.5 parts per thousand of ammonium nitrate were added, in order to favor life conditions of the parasite.

Four days from the date of infection, the first yellow leaves began to appear in a pot belonging to the control group (under a bell jar); and four days later, almost half of the controls showed yellow colored leaves, whereas the plants of the vaccinated groups were normal. After ten days the vaccinated plants, also, began to show signs of distress. After a further period of seven days, the whole of the population of the control plants was dead, while from those treated with heat vaccine six plants survived, and from those treated with ether vaccine two plants survived.

The parallel series kept in the hothouse found better conditions for the plants and less favorable ones for the parasite. Fourteen days after the date of infection, differences were observed between the control, ether vaccine and heat vaccine lots (see Fig. 3, below).

Thirty-two days after the infection, there were small, yellowish, and less numerous plants in the control lots than in the vaccinated lots. Of the latter, the ether vaccine group was the least resistant to infection. The plants, although more numerous and vigorous than those of the controls, were however clearly more backward in development and smaller than those treated with heat vaccine, which were, on the average, much higher (even double) than those of the control group.

APPLICATION TYPE OF VACCINATION

Experiment 1. In view of the positive results obtained during the series of experiments of which, for the sake of brevity, only the modality of two groups has been described, we proceeded with vaccinations in the soil, using vaccines in powder form. In the paragraphs on technique, the procedure followed will be described minutely. For the moment we will call them Dry Vaccine No and Dry Vaccine E. In both cases the vaccination was given in the soil in which the seeds were planted. The experiments were made in the usual way in flower pots of 12 cm. in diameter. Use was made

of normal garden soil sterilized in the dry stove for four hours at 160–170°C. After having filled the pots with soil, and having pressed it down uniformly in order to obtain a regular and smooth surface, the vaccinating powder, mixed with a small quantity of fine soil, was sprinkled on in the desired quantity. This was done in order to obtain a more perfect distribution of the vaccinating powder on the surface of the soil in the pot. After having again lightly pressed down the earth to make the added powder adhere properly, forty seeds per pot were planted. Watering was effected by imbibition so as not to alter the stratification of the vaccine on the soil.

The quantities of vaccine used were:

- 1) control pot
- 2) 0.025 grams of Dry Vaccine No
- 3) 0.100 " " " " "
- 4) 0.200 " " " " "
- (this was destroyed through an accident)
- 5) 0.500 grams of Dry Vaccine No
- 6) control pot
- 7) 0.025 grams of Dry Vaccine E
- 8) 0.500 " " " " "
- 9) 0.100 " " " " "
- 10) 0.200 " " " " "

The pots were left for three days at 30°C. and then, as soon as the seeds began to germinate, were taken into the hothouse and kept at 18–20°C. The vaccinated seedlings showed some signs of suffering, but not to the degree noted in the previous experiments, although the treatment was prolonged for a much greater length of time. Excluding the plants in pot No. 5, for which the dose of vaccine was evidently too high and which were backward in development to the end of the experiment, the others, even as they showed symptoms of disease very slowly, were equally slow in showing signs of recovery. In fact, the experimental infection, made in the same way as in the previously described tests, was effected about two months after the seeds had germinated. The conditions of the plants at seventeen days from the date of infection are shown in figure 4. After a further period of fifteen days, pot No. 1 still had three dying plants, while in the pots numbered 2 and 3 the plants were healthy and vigorous in appearance; but the difference in development between them was slightly decreased, since in No. 5 there were still about fifteen small and suffering plants having a development of about one-third of those in No. 2. The plants in pots 6 and 7 were all dead, while those in pots 8, 9, and 10 were about equal in development, and were healthy and vigorous. These plants, in fact, continued to develop like those in pots 2 and 3 until they had to be destroyed, owing to lack of space.

Experiment 2. The dry vaccines were again used in this test (i.e., No and E); but the method of administration was modified in that, instead of adding the vaccines to the soil with the seeds, they were pulverised (after having mixed them with fine earth) over the already germinated seeds. For each of the pots of 10 cm. in diameter and for every forty seeds, 0.100 grams of powder were used for both vaccines. As controls, three equal-sized pots of 40 non-treated seeds and two pots of 40 seeds vaccinated with 3 cc. of aqueous suspension of heat Thielaviopsis vaccine and ether Thielaviopsis vaccine, respectively, were used.

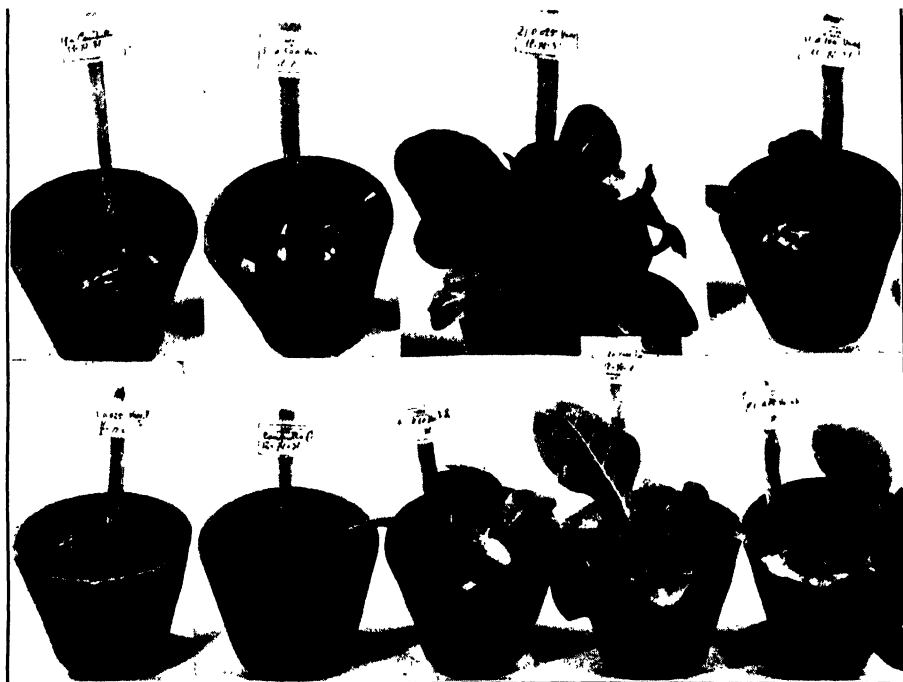


Fig. 4, above. Vaccination with *Dry Vaccine No*—State of the plants 17 days after the infection. The cards above the pots show the various quantities of vaccine used. Fig. 4, below. Vaccination with *Dry Vaccine E*. State of the plants 17 days after the infection. The cards above the pots show the various quantities of vaccine used.

For this series, also, the signs of suffering were but slight, especially in the case of the plants treated with aqueous vaccines. About two months after the vaccination, we proceeded to infect all the pots, following the usual procedure. Thirty-four days later, observations were taken. In the three control pots all the plants were small, rachitic, and chlorotic. On extirpating some, it was noticed that the typical lesions of the collar were present. The plants treated with aqueous vaccines, both of the heat and

of the ether type, were slightly healthier. The most vigorous plants, well developed and healthy, were those treated with Dry Vaccine E; those treated with Dry Vaccine No were slightly inferior in appearance.

Experiment 3. About sixty days after the preparation of the dry vaccines, we made another experiment, using forty plants for each procedure, following the usual technique, and making use of the usual pots. This experiment was for the purpose of testing the state of preservation and activity of the two preparations, which, in the meantime, had been kept in test tubes closed with cotton wool and left on the laboratory bench and therefore in full light. These tests, accompanied by the usual controls, also gave results wholly similar to the previous ones.

TECHNIQUE OF THE PREPARATION OF THE VACCINES

The preparation of the vaccines was carried out, with different techniques, by treating cultures of *Thielaviopsis basicola*. For this purpose the cultures were prepared in large test tubes containing malt broth,⁷ or in flasks of 25 cm. in diameter in those cases where greater quantities of culture were needed. The incubation temperature was that of the laboratory in all cases (18–25°C.). The most suitable age for using the cultures was found to be from ten to fifteen days.

Heat vaccine was prepared as follows: a cultural felt obtained from a culture in malt broth, is pounded in a porcelain mortar with the addition of a little quartz sand (which is afterwards eliminated by decantation) until it is reduced to a creamlike consistency. It is then suspended in an equal part of sterile distilled water. The suspension is then placed for 30 minutes in a water bath, and kept at 70°C., as shown by a thermometer placed in the test tube containing the suspension. Before using this suspension, it is diluted with an equal part of distilled water, shaking carefully both before dilution and before use so as to render it as homogeneous as possible.

Ether vaccine is prepared by careful trituration of the cultural felt of *Thielaviopsis basicola*, as in the case of the preparation of heat vaccine, but without water. The whole is then subjected to the action of ether vapor by placing the material in a thin stratum in a capsule which is kept under a well closed bell jar in which another wide-mouthed vessel containing ethylic ether is placed. Forty-eight hours afterwards, the material thus etherized

⁷ In order to obtain abundant cultures in the large test tubes with ease, it is advisable to allow a streak of agar malt to solidify along the walls of the test tube. The piece of mycelium which serves for planting is placed on this streak. It develops on the agar and thence extends to the surface of the broth. If this expedient is not used, the piece of mycelium easily falls to the bottom of the test tube, and the cultivation of the mould is far more laborious.

becomes more fluid,—evidently by reason of the plasmolizing action of the ether on the mycelium of the microorganism. The only remaining operation is to drive off the whole of the ether which has become fixed. This is done by prolonged heating on the water bath at 37–40°C., followed by evaporation *in vacuo* at room temperature. When the whole of the ether is driven off, the material is diluted with three parts of water (distilled and sterilized), thus obtaining a concentration of mycelium produce equal to that of the heat vaccine.

Dry Vaccine No was prepared from normally cultivated cultures of *Thielaviopsis basicola* finely powdered in a mortar. The material thus obtained was spread in an extremely fine layer on a glass slip which was then heated to 37°C. in the thermostat. In less than 24 hours, the material was perfectly exsiccated. It was then collected with a spatula and left for a further 24 hours at 37°C. Under these conditions, the microorganism is killed, as was proved by cultural tests. For use, the material may be diluted with inert powders, such as fine earth, fine sand, powdered pumice, etc., which it is best to sterilize.

Dry Vaccine E was obtained by triturating the mycelium of *Thielaviopsis basicola* and treating the same with ether, following the same procedure as indicated for the ether vaccine, but without addition of water. The whole is then dried according to the same technique used for the Dry Vaccine No.

RESULTS AND CONCLUSIONS

From these experiments one may conclude that it is possible to increase the resistance of tobacco plants (variety Berkley) against infections by *Thielaviopsis basicola* by treatment with vaccines. The material used as vaccinating substance is obtained from cultures of *Thielaviopsis basicola* and may be prepared by following various procedures. Among these vaccines the type killed with ether and placed in aqueous suspension appears to be the most toxic, although it is the least active in conferring immunity. It is not to be thought that the greater toxicity shown by the ether vaccine is due to traces of ether which have remained attached to the vaccine, because the *Pythium* vaccine, prepared in an exactly similar manner does not produce detectable symptoms of suffering in the plants. The independence of toxic power and of immunizing power in the vaccines is therefore confirmed.

The types of vaccines which have given the best are certain powdered forms. These types have conserved and maintained their activity for two months without special precautions. (They were not examined after a greater length of time.) Of the powdered forms, those obtained by treatment with ether did not have the toxic power shown by the aqueous form,

yet they appeared to exercise an immunizing activity slightly superior to the normal.

The dry vaccines acted equally well whether added to the soil on which the germinating seeds were placed, or administered to seeds already germinated. This fact is in direct contrast to what was observed in the case of the aqueous vaccines, which appear to be less active when added directly to the soil.

The duration, under our experimental conditions, of the state of immunity acquired appears to be about two months. This point of the problem, however, is not clearly determined by our experiments. In order to obtain critical data, it would be necessary to observe numerous lots of plants, treated in various ways, infected at different times, and kept under the best conditions of life as regards surroundings and season. We are convinced, however, that the duration of the immunization obtained under our experimental conditions is sufficient to protect the plants during the early stages of life, which are the stages most freely exposed to the attack of the parasite and during which the plant exhibits the greatest degree of susceptibility.

As a general deduction, it is thought that the theoretical problems involved in the practical vaccination of tobacco plants against *Thielaviopsis basicola* are now sufficiently well in hand that it is desirable to make similar tests on a large scale in practical field cultures. When one considers the minute size of tobacco seeds (100,000 seeds weigh about 6 grams), it is clear that extremely small quantities of vaccinating material are sufficient to affect a large number of plants. Moreover, the preparation of the vaccine calls for a very simple technique whereby it is possible to prepare noteworthy quantities without excessive expense.

We close these notes by advising the reader that our Laboratory can place at the disposal of interested Institutes and private research workers, a certain quantity of vaccine in powdered form which we shall be glad to forward to those who may make request.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1932-1933

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The development of the ascus and the occurrence of giant ascospores in *Coccomyces hiemalis*¹

MYRON P. BACKUS

(WITH TWO TEXT FIGURES AND PLATES 29-32)

This communication is devoted to a study of the development of the ascus in *Coccomyces hiemalis* Higgins on a single host, *Prunus cerasus*. Morphological, cytological, and experimental studies on other phases of development are already well advanced, and it is hoped that these may lead to a full understanding of the life cycle of this species.

Coccomyces hiemalis was first described by B. B. Higgins in 1913. He found the ascocarps of this fungus on the overwintered leaves of *Prunus avium* and by inoculation experiments showed this to be the perfect stage of a *Cylindrosporium* which had often been referred to *C. padi* Karst., and which had long been recognized as the causal organism of the destructive "leaf-spot" disease of sweet cherry. The following year (1914) Higgins was able to demonstrate that this same species is also responsible for "leaf-spot" of *Prunus cerasus* and *P. pennsylvanica*. Keitt (1918) showed that it might in addition attack *Prunus mahaleb*. In his second paper (1914) Higgins outlined the chief morphological features in the development of the fungus, but he made no attempt to study it cytologically.

The order Phacidiales, to which *Coccomyces hiemalis* belongs, is of special interest as a transition group, and but few species in it have yet been subjected to thorough investigation. In only one species has a cytological study of the ascus been made (Jones, 1925). *Coccomyces hiemalis* shows a close resemblance in many features to some of the lichens, a group that has figured prominently in all discussions of the phylogeny of the Ascomycetes, and the study of which, despite several excellent papers dealing with them, may be said to be just getting under way. The presence of prominent trichogynes developing in interesting relation to the numerous microconidia in the cherry leaf-spot fungus especially demands that the phases of development in this organism relating to the initiation of the ascocarp, be subjected to the most careful scrutiny, particularly in view of the apparent homology of these microconidia with the spermatia of the rusts, which have now been shown to be functional elements. Re-

¹ The work here reported was begun while the writer was a graduate student at the University of Wisconsin but was executed largely at the New York Botanical Garden during the tenure of a National Research Fellowship in the Biological Sciences.

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cent demonstrations in the case of certain heterothallic Ascomycetes that the microconidia may function in the capacity of fertilizing agents. (Drayton, 1932; Dodge, 1932; Ames, 1932), are of the greatest interest and significance, and fall into line with the basic idea held by Stahl (1877) and some of the older authors, that the spermatia of the lichen fungi with which they worked, function as fertilizing elements by attaching themselves to trichogynes. In the more recent work, unfortunately, almost no cytological data are yet available.

We do not know whether the cherry leaf-spot fungus is heterothallic or homothallic. However, an experiment which it is hoped may settle this point is under way. It may be of interest here to indicate briefly the methods employed in a preliminary experiment. This first trial has involved the isolation of the eight spores from a single ascus. Since, insofar as we know, ascocarps cannot be produced on artificial media, it was necessary to resort to use of the natural substratum. Large numbers of conidia of each ascospore strain were grown on agar and at the proper time cherry trees were inoculated. The various ascospore strains were used alone and in combination, and the inoculated trees were subsequently kept in isolation. The leaves infected with the fungus were collected at leaf-fall and left out-of-doors in isolation cages over winter. The results of this preliminary trial, which will be detailed elsewhere, have afforded some very interesting clues and have given us some valuable data. They do not settle with certainty, however, the question of heterothallism in this species. Many difficulties beset such an experiment, and many complicating factors are involved. Another experiment based on the information gained from the preliminary test is being conducted on a larger scale and under improved conditions; there is every reason to believe that the question of heterothallism in *Coccomyces hiemalis* can thus be definitely settled.

MATERIALS AND METHODS

The material for the present investigation of the development of the ascus—overwintered leaves of the sour cherry, bearing ascocarps of the “leaf-spot” fungus in various stages—was derived from a variety of sources. Approximately half was collected by the writer during the springs of 1929–’31 at Madison, Wisconsin, in the orchard of the University of Wisconsin and in private orchards in the vicinity. In the fall of 1931, through the co-operation of various plant pathologists and county agents,² I was able to assemble at the New York Botanical Garden infected leaves, collected at the time of leaf-fall, from Penn., N. J., and northwestern N. Y.

² I am indebted in this connection to W. O. Gloyer, W. H. Martin, J. F. Adams, H. H. Whetzel, E. M. Hildebrand, and especially to J. G. Goodrich.

state. These were overwintered at the Botanical Garden and drawn upon as a source of supply for fixations throughout the spring of 1932. I also received from Sturgeon Bay, Wisconsin, and Lockport, N. Y. during April and May 1932, freshly collected leaves that had overwintered in the orchards.³ For still another source of material I am indebted to Prof. G. W. Keitt of the University of Wisconsin who very kindly turned over to me a quantity of imbedded material from his files, representing fixations made by him from orchards near Madison, Wisconsin during the springs of 1915-1917.

In some instances fixation was made immediately after the leaves bearing the fungus were brought into the laboratory and had been washed off, and even occasionally in the field at the time of collection. But for the most part they were allowed to remain in a moist chamber between damp filter papers for varying lengths of time before fixations were made. This was an essential procedure in most cases. The development of the asci of this fungus extends over a considerable period (several weeks, in many cases) and the ascocarps dry out repeatedly during this time. Material brought into the laboratory in a dry state must be placed under conditions favorable for the "recuperation" of the fungus before fixation for cytological study. Fixations were made at from three to seventy-two hours after the leaves were placed in the damp chamber, and two series were made with fixations at two-hour intervals over a 24-hour period.

Flemming's weaker and medium solutions, dilutions of these with equal parts of distilled water, a modification of Flemming's weak with ten times the normal amount of acetic acid recommended to me for fungi by Dr. C. W. Emmons, Carnoy's B, Carnoy's B followed by Flemming's weak, formol-acetic-alcohol, Bouin's, Allen's Modification of Bouin's, Navashin's and Gilson's were among the fixatives tried. Regular Flemming's weak and Flemming's weak diluted one half were found to be about the best of the Flemming mixtures, and were a great deal used. Emmons' modification, tried only in the last fixation series, however, gave results nearly on a par with those obtained with these two other solutions. Allen's modification of Bouin's formol-acetic-alcohol, and Carnoy's B were also employed quite extensively and for certain things were found superior to Flemming's. Sections were cut from four to ten microns thick, the most at six and seven microns. Flemming's triple stain was tried, but Heidenhain's iron-alum haematoxylin, especially with counter-stains of erythrosin or fast green, was found so much superior in general that it was almost exclusively used.

³ E. C. Blodgett and J. G. Goodrich provided me with this material and I am greatly obliged to them for their courtesies.

In addition to the cytological preparations made in the fashion described above, slides of another sort were made for supplementary study. Fresh ascocarpic material was dissected, teased out, and crushed in aceto-carmine. These mounts proved to be very helpful.

NORMAL ASCUS DEVELOPMENT

The time at which asci first begin to form in the spring has been found to vary with the weather conditions. Under the conditions of temperature, etc. which usually prevail in Wisconsin in the vicinity of Madison the first appearance of asci may be expected in the early part of April. It was found, however, that in material overwintered in New York City during the winter of 1931-'32, which was unusually mild and practically snowless, they began to form as early as the middle of March. By bringing leaves inside and leaving them in a moist chamber for a few days asci can sometimes be induced to appear several weeks prior to the time of their formation outside. As has already been pointed out, the development proceeds quite slowly, and it was not until after the middle of May that mature spores were found in abundance under either Wisconsin or New York conditions. Asci in various stages are to be found in a single fruiting body.

In mounts prepared by crushing out young ascocarps in aceto-carmine, it was found quite simple to demonstrate that the asci in *Coccomyces hiemalis* arise by the well-known process of crozier formation. Figures 52-54 show photomicrographs of croziers as seen in such preparations. In good mounts even nuclei can be distinguished. Text-figure 1 shows sketches of typical croziers as observed in these aceto-carmine slides. The tip of the ascogenous hypha bends over (text-fig. 1, A), walls are formed in the familiar fashion, and there can now be observed (pl. 29, fig. 1) a tip cell with its single nucleus and the penultimate cell with two nuclei which proceed almost immediately to fuse (pl. 29, figs. 3-5; also text-fig. 1). In a considerable number of instances the tip cell was seen to have fused back with the antepenultimate cell (text-fig. 1, I, J, K, L, etc.; also pl. 29, fig. 5). But such a cell fusion is apparently not an essential feature for it not infrequently fails to occur (text-fig. 1, N, O, R, etc.). As the penultimate cell grows out to become the young ascus, the fusion nucleus increases in size and moves upward in the elongating sac (text-fig. 1, N, P, and R; also pl. 29, fig. 6). Text figure 1, E and M show interesting situations which might be interpreted as lending support to the theory of Moreau and Moreau (1922; 1928) to the effect that clamp connections occur along ascogenous hyphae. Cases occasionally seen in aceto-carmine slides where the crook cell of a crozier was apparently proliferating to form a short ascogenous branch instead of swelling up to form an ascus

in the usual manner, give us a suggestion of how the situations pictured in the figures just mentioned, may have come about.

Variations in form of the ascus in the leaf-spot fungus are interesting. Some of the asci have very long bases. This is correlated with the fact that in some instances they may arise relatively deep in the stroma. This point will be further discussed in another paper in which the development of the ascogenous system will be specially considered. Despite the general slowness of the asci in maturing, there is evidence that the early stages of growth proceed with comparative rapidity under normal conditions. The young spore sac is usually rather slender and quite evenly filled with dense cytoplasm. The nucleus frequently fills practically the entire cross-

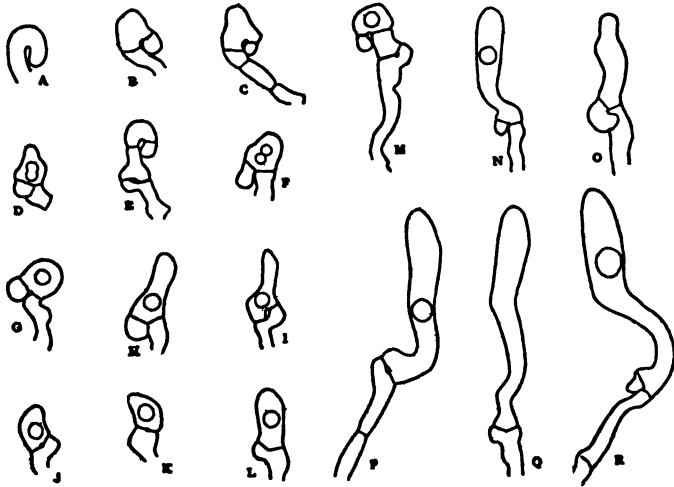


Fig. 1. Croziers and young asci of *C. hiemalis* (from aceto-carmin preparations). Various magnifications.

section of the sac at this stage and may sometimes even be slightly elongated, due apparently to lack of room for it to assume a more spherical contour. Considerable variation exists, however. Plate 29, figure 6, shows an ascus about one-third grown. It shows particularly well the details of nuclear structure to be considered below. It is fairly typical in its general form. As growth proceeds, the ascus continues to swell in its upper portions and takes on the typical clavate form. Once the size shown in plate 29, figures 7 and 8, is attained, there is little further increase until after the spores are formed.

During the growth of the ascus the cytoplasm tends to become aggregated toward the top of the sac especially as the ascus ages. The lowermost regions become practically devoid of stainable contents, while the upper

third of the ascus is seen to be filled with dense, finely granular cytoplasm, the sporeplasm, which in some cases grades off quite imperceptibly into the watery vacuolate epiplasm below, but which usually is quite sharply delimited, especially as the ascus increases in age. Moreover it is rather characteristic for preparations to show invagination of this conspicuous densely-staining mass by the thin plasma below it, a situation sometimes seen in extreme expression as shown in plate 29, figure 13. The dense sporeplasm in the upper part of the ascus is destined to be the seat of activity for the phenomena leading to spore formation.

The large fusion nucleus lies in the dense cytoplasm, often slightly below the center of the mass, and it frequently takes up its position to one side of the ascus (pl. 29, fig. 7). It attains a considerable size—sometimes measuring as much as 7.5μ in diameter. When compared with the definitive nucleus in a form like *Verpa bohemica*, which Komarnitzky (1914) reports has a diameter of up to 16μ , it is not so big, but it is nevertheless a very conspicuous body and is especially striking since the cytoplasm in which it lies is remarkably free from the heavily staining granular material which is so abundant in many Ascomycetes and which I have observed to be very prominent in another Phacidiaceous form, *Diplocarpon Rosae*. Occasionally a few densely stained bodies may be seen, particularly in a zone just outside the nuclear membrane in *Coccomyces hiemalis*, but they are scarce. Exceptionally, several large vacuoles may be present (pl. 29, fig. 7). Numerous big vacuoles are visible in the sporeplasm of the ascus shown in figure 48, which is of interest also because of the fact that in this particular well-grown primary ascus nucleus two relatively small nucleoles are visible. Either the nucleoles of the fusing nuclei failed to unite in this case or perhaps the situation has resulted from fragmentation of a single large nucleole previously present. In any case the example is unique, no others like it having been observed.

The definitive nucleus shows typically a large nucleole, and the chromatin is conspicuous. By far the greatest number of asci observed in the uninucleate condition showed the nuclear network more or less like that shown in plate 29, figs. 7 and 8. This was found to be the case in all of the material, regardless of the fixative used. Since it is already observable (though usually not so clearly defined) in only half-grown asci (fig. 6) and in such predominance among all the asci containing a single nucleus, it is evident that it must represent a considerably protracted stage. The interpretation of the nuclear organization here is not by any means easy. The essential features of it, insofar as I have been able to observe and interpret them, will now be considered.

There is present a framework of clearly distinguishable linen in the

form of a thin thread or threads winding throughout the nuclear cavity, the various portions of which occasionally give the impression of anastomosing with each other; but again in other instances extensive segments appear clearly to lie free in loops (fig. 8, a); very conspicuous beads of chromatin are imbedded in the linin at intervals, (figs. 7 and 8). Just how to interpret the "beads" is not clear. Whether they represent distinct chromatin masses, perhaps of the nature of prochromosomes, or are to be regarded as less definite, possibly chance aggregations in the thread or concentrations at focal points in the framework, of chromatin material in a disperse phase, I am not prepared to say. There is considerable resemblance between the nuclei in *Coccomyces hiemalis* and the figures given us by Bagchee (1925) for *Pustularia bolarioides* where likewise numerous chromatin units figure prominently in the nuclear organization. In this form Bagchee reports the chromatin beads to be very distinct chromatin entities of definite number, perfectly related to the number of chromosomes. She describes the formation of bivalent chromosomes in the pro-phases of the first division by the bringing together of the beads which she designates as "half-univalents," first in pairs and then finally, at the beginning of second contraction, in tetrads. To what extent the chromatin bodies in the nuclei of the cherry leaf-spot fungus are comparable to those in Bagchee's *Pustularia*, I am unable to state. It has not been possible to assign any definite number to these bodies in the species of *Coccomyces* studied. Moreover their size seems to vary, and I could not follow any of the complicated phenomena reported for *Pustularia* as effecting the association of the beads. Nuclei showing clearly defined spiremes also are to be found occasionally (fig. 9). Frequently the spiremes stain quite evenly throughout, but it must be admitted that they sometimes also show suggestions of beads. I have seen suggestions of double threads here, as well as earlier. It seems probable that the stage where chromatin beads are so much in evidence is to be interpreted as a protracted early prophase and that the distinct spiremes represent a later prophase development. It is conceivable that the chromatin bodies might maintain their individuality through this latter stage, although in most cases little trace of them can be found. *Coccomyces* is by no means the most favorable of material for study of these early pro-phases. With the exception of two cases where possible contraction phenomena were indicated, I have been unable to identify in *Coccomyces hiemalis* the ordinary features characterizing the pro-phases of heterotypic division.

It will be remembered that it is characteristic in many Ascomycetes for the fusion nucleus to enter very early into prophase of a heterotypic division. In *Humaria rutilans* Fraser (1908) reported that the nuclei in

the young ascus cell go into prophase independently even before fusion. In *Peziza vesiculosa* where fusion of the nuclei was seen to be delayed until the ascus had attained considerable size, it was also reported (Fraser and Welsford, 1908) that in the material examined the two nuclei were already showing first meiotic contraction at the time they fused. In these and similar forms the fusing nuclei are of quite large size—over 5μ in diameter—and the amount of increase in the size of the fusion nucleus until its maximum is reached is not great. A similar situation obtains in *Phyllactinia corylea* (Harper, 1905). In the species of *Coccomyces* under consideration quite a different situation is found. The nuclei as relatively minute bodies fuse in the crozier without delay. The growth in volume of the definitive nucleus from the time the fusion is completed until maximum size is attained is enormous, paralleling the growth of the ascus in volume (cf. figs. 5 and 7). The small size of the very young primary ascus nucleus, in addition to the difficulties in obtaining good cytological preparations for this stage, renders it impossible to gain any accurate idea of the condition of the chromatin at this time. However, it seems quite unlikely that any such precocious entrance into prophase as Fraser found for *Humaria rutilans* occurs. On the contrary the evidence points to the probability that the fusion nucleus increases to several times its original volume before such stages emerge. These differences in relative size of nuclei at time of fusion and the differences in nuclear activity in these forms are interesting. How far they are to be correlated with mode and rate of development of the ascocarps in the species concerned, should be worth consideration.

We need not consider in great detail the three successive nuclear divisions in the ascus. The division figures here are not large and in general agree in character with figures already published for many other Ascomycetes. In all three divisions the same number of chromosomes—namely, four—seem to be present at the equatorial plate stage. No anaphase stages were seen, and in telophase the individual chromosomes could not, of course, be identified. The spindles were found to be intranuclear, and small densely-staining centrosomes were identified. The spindle of the first division lies more or less parallel to the long axis of the ascus. A division figure at equatorial plate is shown in figure 10. At telophase the chromosomes are grouped in a dense mass at the poles, and a remnant of the spindle usually can be seen lying between the two. The telophase of the first division shows the same features as that of the second, which is illustrated in figure 13, and will be described below. The two reorganized daughter nuclei grow to conspicuous bodies which, like the primary ascus nucleus, show chromatin-bead structure in favorable preparations (fig. 11).

The spindles of the second division lie usually somewhat diagonally in the ascus (fig. 12). Figure 13 shows that the spindles may lie almost parallel to the long axis of the sac. It shows, moreover, an unusually interesting relation of the position of the division figures to the contour of the dense cytoplasm, which is here extremely invaginated. Incidentally it shows also the characteristics of the telophase—the chromosomes closely grouped at the poles and the remnant of the spindle (which elongates somewhat after the nuclear membrane disappears) visible as a rather thick lightly staining thread between them, while in the cytoplasm midway between the two chromosome masses, the disorganizing nucleole of the mother nucleus may still be identified. The position of the nuclei at the four-nucleate stage is indicated in figures 14–16. Chromatin beads can be identified in some cases, but in these smaller nuclei they are usually not clearly distinguishable. Asci at the four-nucleate stage are quite abundant. This fact leads to the assumption that at this point a considerable rest period ensues (cf. observations of Brooks (1910) on *Gnomonia erythrostoma*, Bagchee (1925) on *Pustularia*, etc.). Following the third division (fig. 16) the eight small nuclei move rapidly toward the walls of the ascus and there develop prominent beaks and cut out the spores with the usual accompaniment of astral rays (figs. 18 and 19).

Not very many Ascomycetes with long ascospores have been studied cytologically, and there seems to be some confusion in the literature concerning the exact process by which these spores are developed. Maire's figures (Maire, 1905), showing the very young spores of *Rhytisma acerinum* as more or less spherical or ovoid structures which only later elongate, are doubtless correct. Faull (1912) indicates a similar situation in the development of elongated ascospores in *Laboulbenia chaetophora*, and Jolivet (1910) does likewise in the case of *Geoglossum glabrum*. Lewis' figures for *Pleuraea zygospora* (Lewis, 1911) indicate that here the spores begin as very small, rather broadly ellipsoid bodies which subsequently undergo extensive elongation and finally differentiation. Jones' (1925) figures and description of spore development in *Rhytisma acerinum* are less clear. He suggests the probable functioning of vacuoles in the delimitation process; and one gets the idea from his paper that he believes that the spores as first formed tend to have an elongate shape. The crude figures of Lewton-Brain (1901) for *Cordyceps ophioglossoides*, show the spores delimited as filiform structures.

In my study I have been able to show clearly that in *Coccomyces hiemalis* the spores are cut out as very nearly spherical bodies which only through a process of elongation and growth finally assume the shape typical of the mature spores of this species (see text-fig. 2). In figure 20 the

delimitation process has just been completed. In figures 21 and 22 the spores are older and they stand out in sharper outline. Perhaps there has already been some thickening of the spore membranes. The young spores lie closely packed in the upper part of the ascus, the position previously occupied by the sporeplasm from which they were cut out. The epiplasm is at first dense but thins out as the spores develop. Figure 55 shows an ascus at the stage in question, from an aceto-carminic *in toto* preparation. The normal position of the spores seems to have been upset during the crushing of the ascocarp. But the globular form of the spores in focus is evident.

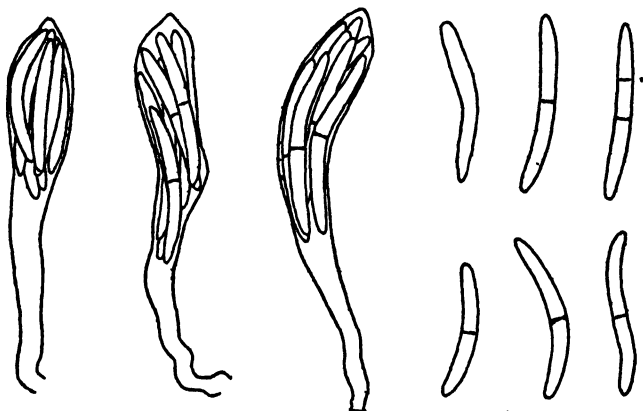


Fig. 2. Asci and ascospores of *C. hiemalis* (from aceto-carminic preparations).
× about 500.

The spores do not long maintain their spherical shape. They very soon start to elongate, increasing slowly in volume. Figures 23 and 24 show two successive sections of an ascus which, although in some respects abnormal, shows clearly the first stages of elongation. This ascus is larger than the average, and the spores are somewhat bigger than usual at this stage. Moreover their usually crowded arrangement is here lacking. Their shape, however, is quite typical. The ascus shown in figure 47 is also abnormal. Here only one of the eight nuclei in the sac appears to have cut out a spore. Remains of several nuclei lying free in the cytoplasm may be seen. Reference will again be made to this ascus in another connection. Figures 25 and 26 show typical asci with the elongation process considerably farther under way. The arrangement of the ascospores is characteristic, remain closely packed together and lie diagonally in the sac, parallel to one another. Often at this stage the exact limits of the individual spores are not easy to see. As the spores attain a considerable length, they slip more and more into a position parallel to the long axis of the sac. The

early elongation apparently takes place with considerable rapidity and although the spores increase in volume, this increase is not often in proportion to the change in length, with the result that the young spores at the stage following that just described, are sometimes quite thin structures (fig. 27). The final stages of elongation take place more slowly; and the spores now increase markedly in diameter while completing their growth in length (figs. 28-31).

Some general idea of the changes in size and shape of the spore nucleus during the development of the ascospores may be had from an examination of figures 20-31. The increase in size from the time the spore is cut out is considerable. As the spore assumes an elongated form, the nucleus also becomes more or less stretched out. In the thinnest young spores the contour of the nucleus may be greatly modified in conformity to the small diameter of the cell in which it lies. The nucleole usually is found near one end of the nucleus, and sometimes that is all that can be clearly distinguished, the stainability of the chromatin varying decidedly, even occasionally in spores of the same ascus (fig. 30). With the increase in diameter of the spore, the nucleus returns more or less to its normal spherical shape (fig. 31).

As the growth of the spore proceeds, the ascus increases in size. The denser materials of the epiplasm are used up more or less completely, and the ascospores usually come to fill the sac in its entire diameter. The fascicled arrangement is typical, and is represented in cross-section in figure 32. I was unable to find nuclear division in spores in any of my material. The evidence is that the original nucleus does usually divide, however; and the spore becomes septated, each segment thus formed including presumably one of the daughter, or grand-daughter, nuclei (figs. 33 and 34). Septation occurs as one of the final steps in the maturation of the spores and is accomplished only a short time before they are shot out. Most often mature spores have a single septum, less commonly two, and quite rarely three. Occasionally non-septate spores may be found (text-fig. 1). There does not appear to be perfect correlation between spore size and degree of septation.

Having thus presented a fairly detailed picture of normal ascus development in *Coccomyces hiemalis*, I shall now consider certain abnormal features.

Giant Ascospores

While studying some mounts of ascocarps dissected and crushed out in aceto-carmin, my attention was occasionally drawn to certain asci which presented an abnormal appearance. While some of the spores in these were perfectly normal, others were seen to be of unusual size and in

some instances of peculiar shape (fig. 57). Closer examination showed, further, that in every instance these asci contained fewer than eight spores. Figure 59 shows the contents of an abnormal six-spored ascus. Two of the spores are markedly longer than the four which are of normal size. The giant spores here differ only in their increased dimensions, whereas one of the two giants in the ascus pictured in figure 57, shows also very abnormal contour. Figure 58 shows what came out of an abnormal five-spored ascus in which the spores were just in process of elongation when crushed. The three central ones are larger than the outer two. Undoubtedly the central three would have elongated and grown to be giants while the other two would have developed into normal spores.

Accounts of the occurrence of giant ascospores are still something of a rarity in the literature. This is perhaps the first time that they have been reported for a parasitic species. Spores of unusual size were occasionally observed by very early mycologists but they were regarded for the most part as inconsequential. Records of irregularity in size and number of spores in an ascus are not wanting in taxonomic literature. Maire (1905), Faull (1905), and Fraser (1908) figured spores of unusual size in *Morchella esculenta*, *Neotiella albocincta*, and *Humaria rutilans* respectively. These early cytologists called attention to the abnormal character of such spores but did not discuss them further. Later workers on big spores have given them more thorough consideration and in several instances, as will be pointed out later, their studies have brought out some very interesting points and relations. Among the best known and most remarkable examples of giant spores are those found in *Neurospora*. Dodge (1927, 1928a, 1928b, 1929) reported their occurrence here in various species and hybrids and indicated their significance in relation to their genetic constitution. Recently Moreau and Moruzi (1932a, 1932b, 1932c) have described some interesting experiments they performed with big spores found in *N. sitophila*. Abnormally large ascospores are also known in *Pleuroge anserina* and have been found comparable to those of *Neurospora tetrasperma*. Moreau (1914) has called attention to variability of ascospore size in *Bulgaria inquinans* and has presented an interesting study of the situation there. Very recently Zickler has produced giant spores experimentally in *Sordaria macrospora* and *Neurospora crassa* by the use of chloral hydrate and ether. In most of the instances evidence, either direct or indirect, has been brought out to the effect that more than a single nucleus is included in each giant spore at the time of its formation. Fraser (1908) figured five nuclei cooperating in the cutting out of a single giant spore in *Humaria granulata*, and Faull's (1905) drawing of the big *Neotiella* spore shows that two nuclei were included. Maire (1905) found evidence that

likewise two nuclei were involved in the formation of the big *Morchella* spore which he figured. In 1907 Dangeard published a drawing of an ascus of *Ascobolus furfuraceus* with seven spores, one of which contained two nuclei. Very recently Gwynne-Vaughan (1933) has figured a six-spored ascus of *Lachnea scutellata*; one of the six spores is an irregularly shaped giant with three nuclei. Dodge has shown clearly that a correlation exists between the number of spores found in an ascus in *Neurospora* and the presence among them of spores of unusual size, and a similar correlation is known to exist in *Pleuraea anserina*, etc. "Extra-giant" spores have been found in *Neurospora* (Dodge, 1927, 1928a; Moreau et Moruzi, 1932a), and recently they have been artificially produced by Zickler (1931) especially in *Sordaria macrospora*. An extreme case where but one super-giant *Neurospora* spore is produced in an ascus, is figured by Dodge (1928a) who believes that in such a case the giant has claimed all eight nuclei present in the sac.

A paper of interest and one in which evidence is brought forth that the inequality in size among spores in an ascus may not necessarily be correlated with a difference in nuclear content at the time the spores are cut out is that of Moreau (1914), above mentioned, on *Bulgaria inquinans*, a species where irregularities in number and especially size of spores has apparently been recognized quite widely. Moreau concluded from his study that in some instances two or three nuclei are included in a single big spore, in which event the total number of spores is proportionally reduced. However, he discovered that not all the big spores were of this same cytological character. Some asci contained some big and some small spores but regardless of their size each contained only a single nucleus. The explanation for this was found to lie in the fact that there is a tendency in this species to a lack of synchrony in the nuclear divisions in the ascus. Because of this situation some spores (usually 4) are formed before the others. The assumption is that the first-formed spores are better nourished and hence grow bigger. The later-formed spores are usually perfectly viable, however. Such asci naturally contain eight spores. But in some instances the spores last cut out may be so poorly nourished that they abort, and in such a case superficial examination may show the presence of only four spores. In this species, then, the number and size of ascospores may both vary for quite different reasons.

There are to be found in the literature descriptions of other species which agree more or less closely with the form just described in showing, very frequently, asci with four large and four small spores. In two species of *Trichoglossum*, *T. velutipes* and *T. tetrasporum*, Sinden and Fitzpatrick (1930) have described a situation where only four spores in an ascus mature

and the other four degenerate after formation or remain more or less abortive. Woronin (1888) described and figured the asci of *Sclerotinia oxycocci* and *Sclerotinia baccarum*. In both of these he found, apparently with considerable constancy, four large ascospores in each spore sac and also four of much smaller size. Unlike the situation in the species of *Bulgaria* which Moreau studied, however, Woronin reported that the small spores in the *Sclerotinias* in question would not germinate. Unfortunately we know nothing of the cytology of the ascus either in the case of these forms described by Woronin or of the two *Trichoglossum* species above mentioned. It would be interesting to determine whether the situations here are to be explained in the same fashion as that in *Bulgaria inquinans*. There can be no doubt that nutritional relations may play a very significant part in causing variations in ascospore size. In the light of this and of our knowledge of degeneration of nuclei and spore initials under a variety of circumstances, it is apparent that without cytological study we cannot safely come to a conclusion as to the number of nuclei included in any particular spore.

I have mentioned the fact that in the cherry leaf-spot fungus, as also in some other regularly eight-spored forms, it has been ascertained that asci in which big spores occur have fewer than the normal number of spores. In several forms, as in certain species of the Erysiphaceae, *Laboulbenia*, *Meliola*, and *Keithia*, also in *Neurospora tetrasperma*, *Pleurage anserina*, etc. it is the rule. The cytological studies in which the nuclear relations in these forms are considered are of interest here because the nuclear phenomena in relation to spore formation in many of these are of the same order as those involved in the formation of giant spores. In fact, one might say that in a certain few of these forms all the spores are giants and that these are formed in definite number and regular fashion, the habit of forming them having become established as a constant character in the particular species. All except the most recent of these studies have been noted by Dodge (1928b).

Harper (1905) studied *Phyllactinia corylea* which usually shows two spores in an ascus and found that although the usual eight nuclei are formed, six degenerate and only two cut out a spore each. In the two species of *Laboulbenia* studied by Faull, *L. chaetophora* and *L. gyrinidarum*, four of the nuclei function and four degenerate, each of the four spores formed thus having a single nucleus at its initiation. Komarnitzky (1914) concluded that in *Verpa bohemica* the two spores developed each include but a single nucleus. He found that the regular triple nuclear division occurs in the ascus but reports that in his material following each of the first two divisions one of the daughter nuclei migrated out of the dense

sporeplasm into the more watery cytoplasm below, there to degenerate directly or undergo a division after which the resultant daughter nuclei would disorganize—an interesting sequence if true, but unfortunately Komarnitzky's figures are not completely convincing. We know of other forms where the reduced number of spores is due to degeneration of spore initials after they have been formed.

Podospora anserina (*Pleurage anserina*) (Wolf, 1912), which has typically four spores, was the first form in which the inclusion of more than one nucleus was reported as a phenomenon of regular occurrence. Eight nuclei are formed in the ascus and two co-operate to form each spore. Dodge (1927) found a similar situation in the four-spored species *Neurospora tetrasperma*, but he made a more complete cytological study of the ascus and gave us very interesting figures showing the actual details of spore delimitation with two nuclei co-operating. Moreover he was able to offer conclusive evidence that in that species nuclei of opposite "sex" come together in pairs, and each pair cuts out a spore capable at maturity of germinating to produce a homothallic mycelium. Dwarf spores formed as an abnormality and containing a single nucleus at origin, were found to be of one "sex" or the other. Such a spore produced a mycelium which, unless mated with the opposite strain, remained sterile. A similar state of affairs apparently exists in the four-spored form *Pleurage anserina* (Dowding, 1931), and likewise in the four-spored form of *Sordaria fimicola* (Page, 1933). Recently Graff (1932) has shown that two nuclei are included in each of the four spores of the ascus in *Meliola circinans*. In some ways the most remarkable case is that reported by Dodge (1928b) for *Keithia chamaecyparissi* where he concluded that despite the fact that only two spores are regularly formed, all eight nuclei function, four being included in each ascospore.

Our knowledge of the nuclear situation in giant spores in Ascomycetes has been arrived at not only through actual cytological observation, but also to some extent by deduction from certain cultural experiments in which the character of mycelia derived from big spores has been studied. In *Neurospora* which has played a major rôle in the giant spore studies, deductions of this kind have had an important part (Dodge, 1929, Moreau and Moruzi, 1932a; 1932b).

In the case of giant spores in *Coccomyces hiemalis* I was fortunate in obtaining some cytological data concerning the nuclear situation, which, although not complete is nevertheless interesting. In studying a relatively large number of cytological preparations of sections through ascocarps, occasionally I found an ascus with giant spores. Although thus far I have been unable to construct a complete developmental series from this scat-

tered material, yet evidence is clear that the big spores in this form claim at their formation two or more of the eight nuclei resulting from the three successive nuclear divisions. I have found to date no examples of giant spores in process of being delimited. Figure 35, however, shows an ascus where the spores have not yet begun to elongate. There are seven spores present and one of them is considerably larger than the others and contains two nuclei. In figure 36 are to be seen two more spores of interest. Comparison of their size with that of normal spores in the spherical stage at once shows these to be giants. In one of the spores—the larger of the two—there are three nuclei, while the other has two. Figure 37 shows two giant spores in early stages of elongation, each containing two nuclei. Figure 39 shows a clearly abnormal spore which, however, is apparently not yet fully grown. This giant shows an atypical shape and contains five nuclei. In figures 38 and 40 can be seen a two- and three-nucleate spore respectively. The contrast in size with normal spores is here well illustrated. The giant pictured in figure 42 shows four nuclei. But its great size would suggest that perhaps even more were present but were cut off in the sectioning. Unfortunately the rest of the ascus could not be identified in the next section. Figures 41 and 43 are of interest because of the peculiar shape of the big spores; and incidentally the spore shown in figure 43 contains six nuclei—the largest number I have observed to date. It should be pointed out that while the included nuclei may take up various positions in a big spore, as inspection of the figures will show, there seems to be a decided tendency in many cases for the nuclei to clump closely together (figs. 39, 42, 43, 45, and 46).

In certain of these asci with big spores a nucleus can be seen occasionally which has not to all appearances been included in any spore but lies free in the epiplasm, as is so common in the powdery mildews. These examples are quite rare in my material. Mention has already been made in the preceding section, of an ascus obviously not normal but without big spores where most of the nuclei seemed destined to disintegration (fig. 47). The development of all these abnormal asci may likely be perfectly normal up to a certain stage. It may well be that at some critical point adverse environmental factors of one sort or another (perhaps of small moment) obtaining at the time, disturb the delicately-balanced workings in the spore sac. This upset might conceivably be expressed in more than one way. Dodge (1928a) has given us a most interesting figure of a case in a *Neurospora* hybrid where an ascus failed to develop any spores at all but instead the wall of the ascus darkened and took on the normal markings of a mature spore. Zickler (1931) in his work seems to have obtained similar cases where whole asci took on features characteristic of mature spores.

It may not be exactly correct to speak of these in the fashion that Zickler does, as asci which have turned into single big spores. The fundamental thing here, however, seems to be that the protoplasts, although failing to function in the usual fashion, do not abort completely or disintegrate, but, with age, effect certain changes in the whole sac which normally characterize maturation phenomena in spores of the species involved. It is quite conceivable that in these cases the plasma membrane of the ascus may function exactly as the limiting membrane formed when a spore is cut out. In a certain sense, then, it may be right to speak of the transformation of one of these sacs into a single spore. But we must distinguish carefully between these types and such examples as Dodge (1928a) figures where we have a single clearly defined super-giant spore lying free in the sac, a spore very evidently delimited in the fashion characteristic of ascospores, though all the nuclei must have co-operated in the process. Zickler fails to distinguish sharply between the two types. Nothing is known of the nuclear behavior in the asci undergoing the peculiar changes just described, and none of these "asci" has ever been germinated. In any case these examples furnish us with extreme illustrations of drastic modifications of the familiar sequence of events in the spore sac, correlated doubtless with some serious upset in the mechanism. Zickler's success in producing asci with big spores in abundance by use of certain chemicals is very interesting and may open the way for an extensive and illuminating study of experimental abnormal cytology of the ascus.

In general, on the basis of the facts disclosed in the study of the cytology of the giant spores in the leaf-spot fungus, as already detailed, I believe we are safe in concluding that in *Coccomyces* the observation that there are fewer than eight spores in asci containing spores of unusual size is to be explained by the fact that the giants enclose two or more of the eight nuclei which are present as the result of the three successive nuclear divisions.

I have been unable to find any septate giant ascospores, so I cannot be sure that they ever do become septate. If they do, it would be interesting to learn the nuclear behavior associated with septation. Also no big spores have to date been germinated. If these can be germinated, as is likely, it would be worthwhile to study the nuclear behavior during the process. The situation here is especially interesting because of the fact that the mycelium in this species is made up of uninucleate cells.

We are not yet in a position to evaluate the significance of giant spores in *Coccomyces hiemalis*. They are of interest of course as abnormalities. The observations here recorded place the cherry leaf-spot fungus among the few species, still less than ten, in which giant ascospores have been

reported. They place it in the still more limited list of normally eight-spored forms where giant spores have occasionally been found and in which convincing evidence has been adduced that more than a single nucleus is involved in the formation of each of these. We have here the first parasitic form and the first long-spored form recorded as exhibiting the phenomenon.

If this species could be shown to be heterothallic and of the type we know in *Neurospora sitophila* in which it has been demonstrated a definite segregation takes place, so that four spores of one "sexual reaction" and four of another are formed in every normal ascus, we should be able then to determine experimentally the compatibility relations of the big spores. In such a case, giant spores containing five or six nuclei, such as I have been able to observe, would surely contain nuclei of opposite "sexual reactions," and a homothallic mycelium might perhaps be expected to result when such a spore germinated, just as Moreau and Moruzi (1932a) found that in *Neurospora sitophila* certain giant spores produced a mycelium that by itself developed perithecia, although a normal sized spore in this species invariably produces a mycelium of one "sexual" reaction only.

SUMMARY

1. Origin of the asci through crozier formation is here described for *Coccomyces hiemalis*.

2. The definitive nucleus shows a protracted prophase stage in which chromatin beads are prominent.

3. The division figures show the features commonly described for nuclear divisions in asci. Four chromosomes seem to be present at equatorial plate in all three divisions.

4. Following the last division the nuclei develop prominent beaks, and the spores are delimited with the usual accompaniment of astral rays.

5. The ascospores are cut out as practically spherical bodies and only after a period of elongation and growth attain the form characteristic of mature spores in this species.

6. The occasional occurrence of asci with giant spores is reported. It has been possible to show, especially in aceto-carmin preparations, that such abnormal asci contain fewer than eight spores.

7. Evidence is presented on the basis of a cytological study that two or more of the eight nuclei present in the ascus following the third nuclear division are incorporated in each giant spore at the time it is delimited. Big spores containing from two to six nuclei are described. The possible significance of such abnormal ascospores is indicated.

I take much pleasure in expressing my indebtedness to Prof. E. M. Gilbert who suggested this study and guided it through its early stages, and especially to Dr. B. O. Dodge who sponsored the major portion of the work, during my tenure of a National Research Fellowship, and who gave most generously of his time and helpful advice. Thanks are also due Prof. R. A. Harper for examining some of the preparations, for his valuable advice on certain points, and for criticism of the manuscript. I wish in addition to express my gratitude to Prof. G. W. Keitt for his kind co-operation in providing certain materials for this study and for his sympathetic interest in the progress of the work.

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Explanation of plates

All drawings were made with the aid of an Abbe camera lucida. All except Fig. 19, Plate 29, were drawn under a Leitz 12 oil imm. lens with Leitz ocular 4. Magnification about 1400 diameters. For Fig. 19 a Zeiss 20 \times ocular was used; magnification obtained approximately 2900 diameters. The photomicrographs were taken at various magnifications.

Plate 29

Figs. 1-5. Croziers.

Fig. 6. Young ascus about one third grown.

Figs. 7 and 8. Uninucleate asci, showing prominent chromatin bodies in nuclei.

Fig. 9. Spireme.

Fig. 10. First division, equatorial plate.

Fig. 11. Two-nucleate ascus, nuclei showing "chromatin beads."

Fig. 12. Second division, equatorial plate.

Fig. 13. Second division, telophase; ascus showing invaginated spore-plasm.

Figs. 14 and 15. Four-nucleate stage.

Fig. 16. Third division.

Fig. 17. Eight-nucleate stage.

Fig. 18. The delimitation of the spores.

Fig. 19. Beaked nucleus and cutting-out of a spore. \times about 2900.

Plate 30

Fig. 20. Spores just cut out.

Figs. 21 and 22. Stage following that in fig. 20. Spores still spherical.

Figs. 23 and 24. Two sections of same ascus. Earliest stage of elongation of ascospores. Ascus abnormally large.

Figs. 25 and 26. Early stages in elongation of ascospores.

Fig. 27. Ascus with young, very narrow, elongated spores.

Figs. 28-30. Further stages in growth and elongation of ascospores.

Fig. 31. Late stage in development of spore in uninucleate condition. The nucleus has returned to a nearly spherical shape.

Fig. 32. Cross-section of a maturing ascus, showing spore arrangement.

Fig. 33. Ascus with septate spores.

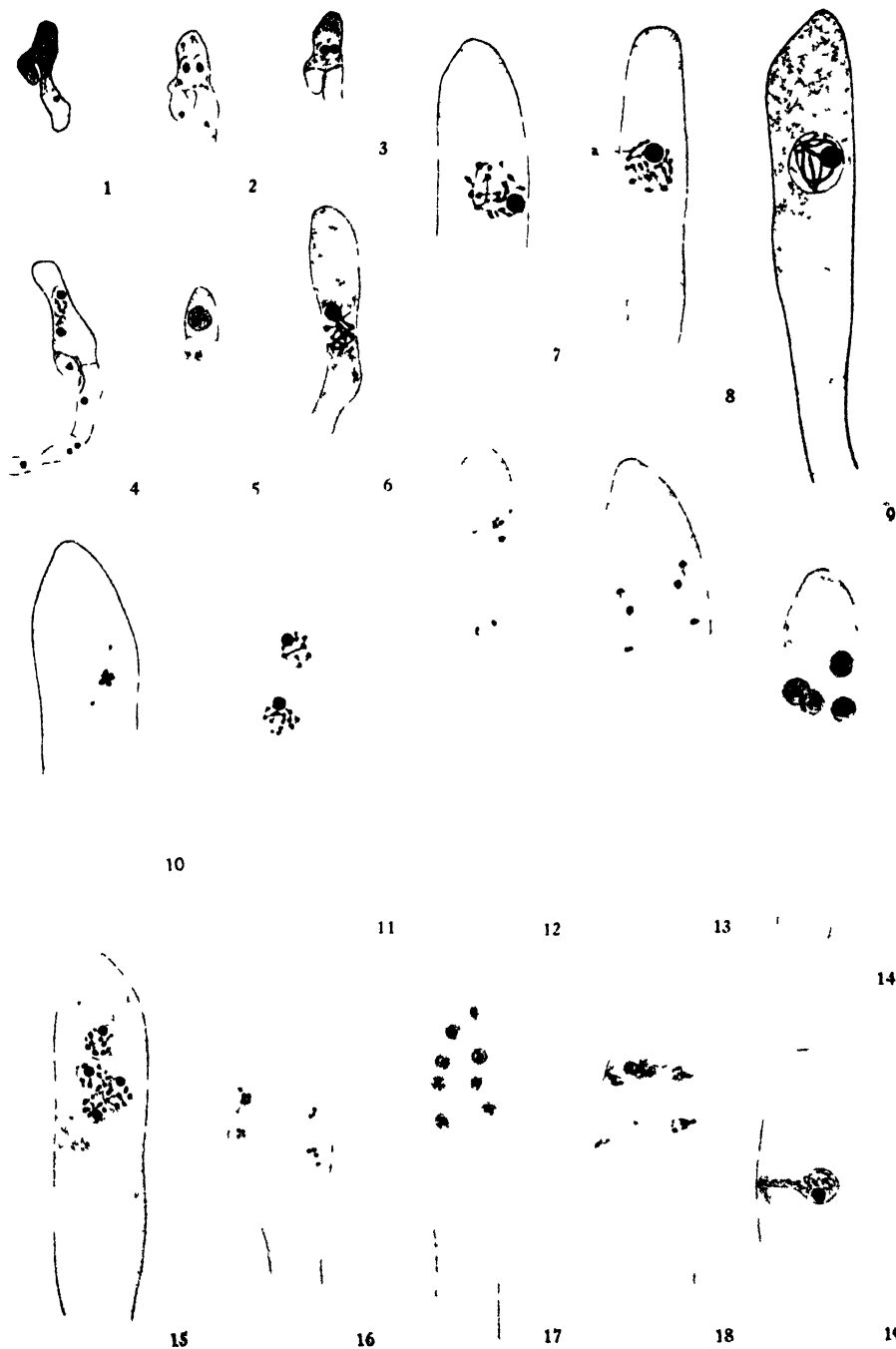
Fig. 34. Mature septate spore.

Plate 31

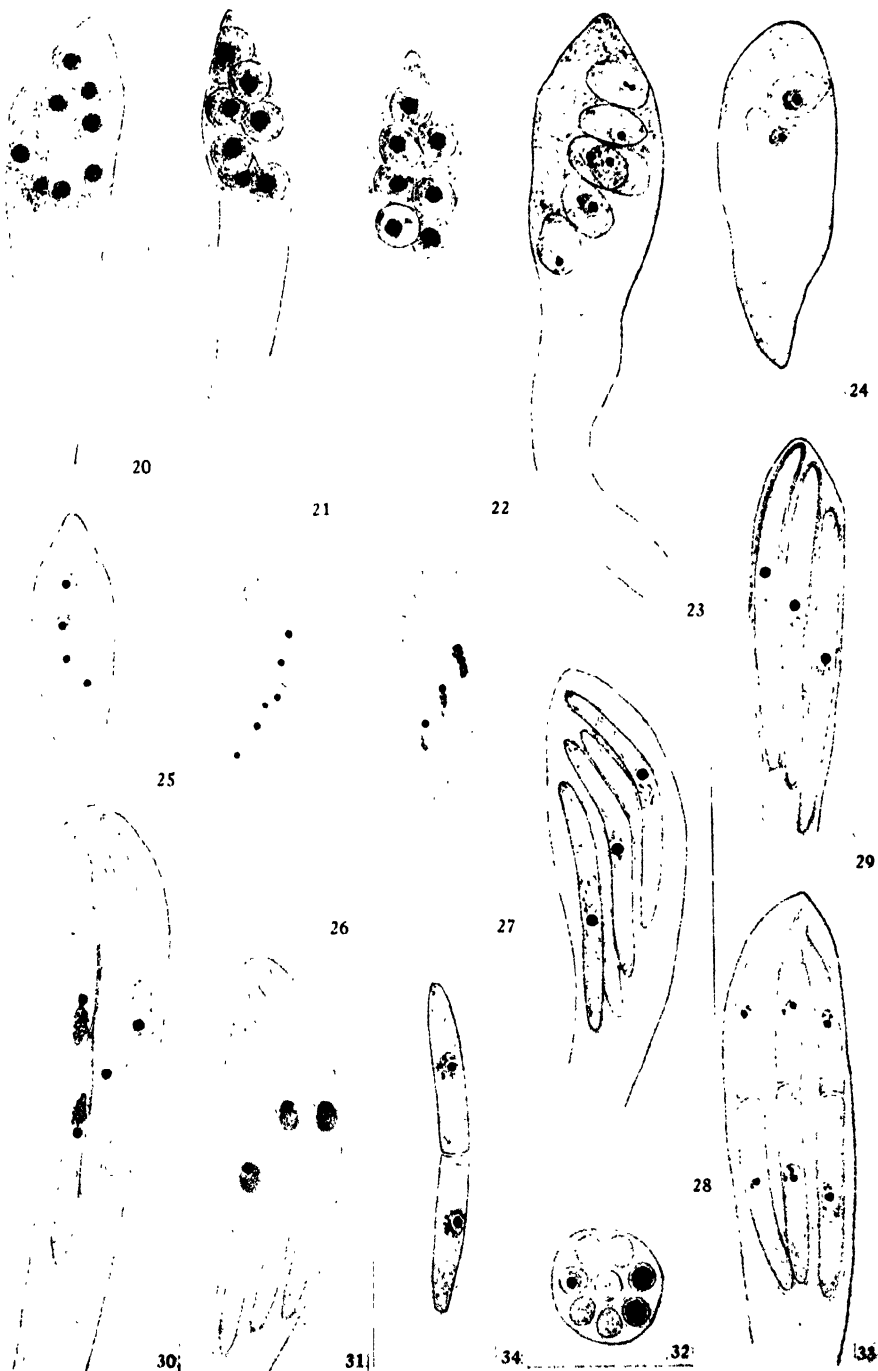
- Fig. 35. Seven-spored ascus shortly after delimitation of spores. One spore a two-nucleate giant.
- Fig. 36. Ascus with two young giant spores.
- Fig. 37. Two giant spores in early stage of elongation.
- Fig. 38. Two-nucleate big spore.
- Fig. 39. Five-nucleate giant of atypical shape and not full-grown.
- Fig. 40. Section of ascus showing one three-nucleate giant and three normal spores.
- Fig. 41. Three-nucleate spore of atypical form.
- Fig. 42. Four-nucleate giant spore.
- Fig. 43. Six-nucleate spore of irregular shape.
- Fig. 44. Portion of an ascus showing part of a big spore with two nuclei.
- Fig. 45. Portion of a giant spore showing three nuclei clumped together.
- Fig. 46. Portion of a three-nucleate big spore with clumped nuclei.
- Fig. 47. Abnormal ascus. A single spore just beginning to elongate, and nuclei lying free in the epiplasm.
- Fig. 48. Ascus showing two small nucleoles in fusion nucleus. Note also vacuolate sporeplasm.

Plate 32

- Fig. 49. Section of an unopened ascocarp showing general features. Largest asci in uninucleate condition.
- Fig. 50. Section of two open apothecia. Spores elongated and nearly mature.
- Fig. 51. Portions of contents of an ascocarp crushed out in aceto-carmin.
- Figs. 52-54. Photomicrographs of croziers from aceto-carmin preparations.
- Fig. 55. Photomicrograph of ascus showing spores in spherical stage.
- Fig. 56. Photomicrographs from aceto-carmin preparations, illustrating growth and maturation of ascospores. A, B, and C taken at same magnification. (\times about 400.)
- A—Ascus with spores in relatively early stage of elongation. Note condition of epiplasm.
- B—Ascus with spores further developed.
- C—A mature spore.
- Fig. 57. Abnormal ascus showing two giants, one, especially, of atypical shape.
- Fig. 58. Contents of abnormal five-spored ascus with spores in process of elongation. Three giants and two normal spores.
- Fig. 59. Contents of an abnormal ascus: two giant spores and four normal spores.



BACKUS COCCOMYCES





BACKUS COCCOMYCES



BACKUS. COCCOMYCES

On *Poa malabarica* Linnaeus

E. D. MERRILL

An interesting case of interpretation of types is presented by *Poa malabarica* Linn., regarding which there may well be differences of opinion. The species has been reduced to as diverse ones as *Panicum nodosum* Kunth (*P. arnottianum* Nees) = *Hemigymnia* = *Ottlochloa*; by an error in identification to *Centotheca lappacea* Desv. = *C. latifolia* (Osbeck) Trin.; and to *Diplachne fusca* Beauv. The case seems to be worthy of more extended consideration than has been given it. Munro (Jour. Linn. Soc. Bot. 6: 43. 1862) stated that the specimen of *Poa malabarica* in the Linnaean herbarium is *Panicum arnottianum* Nees. This was noted by me (Philip. Journ. Sci. Bot. 4: 248. 1909) when I transferred the specific name to *Panicum* as *P. malabaricum* (Linn.) Merr., on the assumption that this specimen was the actual type. At this time, on the basis of a rough tracing of Rheede's illustration, I considered that his plate of *Tsiamapulu* represented the same species as the specimen in the Linnaean herbarium that had been examined by Munro. This is not the case, however, as noted by Stapf (in Prain Fl. Trop. Afr. 9: 743. 1920) who there proposed the generic name *Hemigymnia* to include *Panicum multinode* Presl = *P. nodosum* Kunth and *P. arnottianum* Nees. Hooker f. referred Rheede's illustration, cited by Linnaeus in the original description of *Poa malabarica* Linn. to *Diplachne fusca* Beauv. and Stapf thus accepts this: "What Rheede's plate represents may be doubtful but I would suggest that it was drawn from a specimen of *Diplachne fusca*." It unquestionably represents Beauvois' species.

In 1930 Henrard (Meded. Rijks Herb. Leiden 61: 12. 1930) after examining the specimen of *Poa malabarica* Linn. in the Linnaean herbarium, concluded that it represented a species distinct from both *Panicum nodosum* Kunth and *P. arnottianum* Nees, and transferred the specific name to *Hemigymnia* as *H. malabarica* (Linn.) Henrard for a species known only from southeastern China and Indo-China. A year later Dandy (Jour. Bot. 69: 54. 1931) proposed the new generic name *Ottlochloa* for *Hemigymnia* Stapf, non Griff., with the binomial *Ottlochloa malabarica* (Linn.) Dandy for the southeastern Asiatic form. Stapf, Henrard and Dandy all assumed that the actual specimen in the Linnaean herbarium, one collected by Osbeck near Canton, China, was the actual type of *Poa malabarica* Linn. I do not accept this interpretation as, even with Linnaeus' wide concept of geographic areas as appertaining to "India," I consider it illogical to typify a species bearing the name *malabarica* by a specimen collected in southeastern China, and a form that does not occur in Malabar,

or even in India, and one that does not conform to the characters given by Linnaeus.

The original Linnaean description of *Poa malabarica* is as follows:

"*Poa paniculae ramis simplicissimis, floribus sessilibus, seminibus distantibus, culmo repente. Tsiamapulu Rheed. mal. 12. p. 83. t. 45. Habitat in Indiae arenosis.*"

It may be noted that Linnaeus took his specific name, all the characters, except possibly "*culmo repente*," and the habitat from Rheede who states as to the habitat: "*Planta arenosa gaudens solo*," and as to the spikelets "*spicae . . . oblongae, cuspidatae . . . quatuor constantes foliis cuspidatis, in singulis semen includitur unicum.*" These characters are not those of *Panicum* (*Hemigymnia*, *Otlochlora*), but apply to *Diplachne*, and the illustration clearly represents *Diplachne*; nor does the Linnaean phrase "*seminibus distantibus*" apply to *Panicum*, while the habitat cited is not that of *Panicum nodosum*. Yet Stapf states that this description was based on the specimen in the Linnaean herbarium, not on Rheede's illustration. He considers that Linnaeus' quotation of the reference to Rheede is of little importance in this instance and explains the habitat "*in Indiae arenosis*" by the loose way in which the term India was used in those days or as a consequence of Linnaeus' mistaken identification of the plant of Rheede.

In tracing the history of the specimen in the Linnaean herbarium, which was in the herbarium in 1753, when the first edition of the *Species Plantarum* was published and which was named *Poa malabarica* by Linnaeus himself, it is found that this was collected by Osbeck in the vicinity of Canton, China, December 17, 1751, as recorded by Osbeck himself. He reached Sweden on his return trip to Europe on June 26, 1752. It is probable that his botanical material was delivered to Linnaeus shortly after he reached home, for some species based on Osbeck's specimens are included in the first edition of the *Species Plantarum* (1753).

It is clear that in June 1752 the manuscript of the *Species Plantarum* was well advanced and that these Osbeck references were interpolated in the manuscript or in the text. It seems also safe to assume that the entire original basis of *Poa malabarica* Linn., at least as to the original manuscript, was the illustration and description cited from Rheede's *Hortus Malabaricus*; that the erroneous identification of Osbeck's specimen as representing *Poa malabarica* was hurriedly done; and that perhaps the phrase "*culmo repente*" was added from the actual specimen. In view of these circumstances, and particularly in view of the Linnaean description, and the fact that his concept of *Poa* included *Eragrostis*, but nothing ap-

proaching *Panicum*, I do not accept the named specimen in the Linnaean herbarium as the actual type of *Poa malabarica*, but interpret the species wholly from Rheede's illustration and description; the specimen merely represents an erroneous identification on the part of Linnaeus. That he noted the error is evidenced by the fact that in repeating the description, Species Plantarum ed. 2, 100. 1762, he eliminated the reference to Rheede but did not otherwise modify it, so this description does not apply to the *Panicum* (*Hemigymnia*, *Ottlochloa*), even the "seminibus distantibus" remaining as in the original. Neither here nor in the original description does Linnaeus cite the Osbeck specimen, or China as a habitat, nor is there any indication in the description, except possibly the "culmo repente," that it was based on an actual specimen. The case might be disposed of under the rule that a description based on a mixture of two or more species is invalid, but I personally prefer to interpret this Linnaean species on the basis of the description and illustration cited by him, ignoring the specimen as erroneously named. The partial synonymy would then be as follows:

Diplachne malabarica (Linn.) comb. nov.

Poa malabarica Linn. Sp. Pl. 69. 1753, quoad syn. Rheede, excl. spec. in herb. Linn.
Festuca fusca Linn. Fl. Palaest. 13. 1756, *nomen nudum*, Amoen. Acad. 4: 450. 1759,
nomen nudum, Syst. ed. 10, 876. 1759, Sp. Pl. 109. 1762.

Bromus polystachios Forsk. Fl. Aeg.-Arab. 23. 1775.

Festuca indica Retz. Obs. 4: 21. 1786.

Triodia ambigua R. Br. Prodr. 183. 1810.

Diplachne fusca Beauv. Agrost. 163. 1812.

Poa procera Roxb. Fl. Ind. 1: 334. 1820.

Diplachne indica Spreng. Syst. 1: 351. 1825.

Leptochloa? fusca Kunth Distr. Méth. Gram. 91. 1829.

Uralepis fusca Steud. Syn. Gram. 247. 1854.

Uralepis drummondii Steud. l. c. 247. 1854.

Eragrostis procera Steud. op. cit. 266. 1854.

Diplachne polystachya Backer in Bull. Jard. Bot.
Buitenz. III. 2: 325. 1920.

Backer notes (Bull. Jard. Bot. Buitenz. III. 2: 325. 1920), that *Festuca fusca* Linn. (Sp. Pl. ed. 2, 109. 1762) the name bringing synonym of *Diplachne fusca* Beauv., was described from a Palestine specimen as having a decompound panicle with 16- to 24-flowered spikelets about an inch long and because these are not characters of *Diplachne fusca* Beauv. he abandoned the Linnaean specific name and accepted for the common and widely distributed grass currently referred to *Diplachne fusca* (Linn.) Beauv. the binomial *Diplachne polystachya* Backer, based on *Bromus*

polystachios Forsk. (1775). In *Diplachne fusca* Beauv. as currently interpreted the spikelets are usually less than 1 cm long and bear from 4 to 16 florets. At my request Mr. J. E. Dandy of the British Museum, Natural History, examined the Linnaean type and reports as follows:

"I have examined Linnaeus's type-specimen of *Festuca fusca* at the Linnean Herbarium, and am of the opinion that it is conspecific with the grass currently passing as *Diplachne fusca*. Linnaeus's description, Sp. Pl. ed. 2, is misleading. I counted the florets in a few spikelets of the type and found 8-11 florets to a spikelet. Linnaeus stated that there were 16-24, but I suspect that he counted the florets of two spikelets which happened to be lying end to end; at any rate he certainly miscounted them. The type-sheet bears the written sign \ominus which means that the specimen was collected by F. Hasselquist (in Palestine). The epithet *fusca* is written at the bottom of the sheet. Incidentally the name *F. fusca* was first published (as a nomen nudum) by Linnaeus in 1756 and a description first appeared in 1759. The full reference is as follows: *Festuca fusca* L., Fl. Palaest. 13, nomen nudum (1756); Amoen. Acad. 4: 450, 1759, nomen nudum; Syst. Nat. Ed. 10, 2: 876. (1759); Sp. Pl. Ed. 2, 1: 109. (1762)."

Some may object to this interpretation because Rheedé's rather crude figure shows distant obtuse glumes, more like those of some species of *Eragrostis*; yet his description calls for cuspidate glumes, and while the spikelets are described as having four "foliolis" the figure actually shows 5 to 9 glumes. Hooker f. (Fl. Brit. Ind. 7: 329. 1897) and in Trimen (Fl. Ceyl. 5: 300. 1900) reduced Rheedé's illustration Hort. Malabar. 12: pl. 45, to *Diplachne fusca* Beauv. and I accept this as correct, yet in so doing it involves the new combination made above.

As noted above, Stapf proposed the new generic name *Hemigymnia* in 1920 to include *Panicum multinode* Presl = *P. nodosum* Kunth, and *P. arnottianum* Nees. On the basis that this name was invalidated by the earlier *Hemigymnia* Griff., Dandy proposed the new name *Ottochloa* in 1931. If a distinct genus be represented, Dandy's name should be accepted. The difference between *Ottochloa* (*Hemigymnia*) and *Panicum* are so slight that I see little reason for maintaining this small group as generally distinct and accordingly here consider the species under *Panicum* in my present discussion of certain nomenclatural problems involved.

Stapf, followed by E. G. and A. Camus, recognized *Hemigymnia multinodis* Stapf and *H. arnottiana* Stapf as representing distinct species. When I erroneously accepted the Linnaean name under *Panicum malabaricum*, I referred to it the large form with ample panicles, retaining *Panicum nodosum* Kunth, the common Philippine plant with rather small panicles, as a distinct species. The two species, *Panicum "malabaricum"* and *P.*

nodosum, were recognized in my Enum. Philip. Fl. Pl. 1: 65. 1923. I do not detect any sufficiently well marked constant differences between the typical Indian *Panicum arnottianum* Nees and the Philippine *Panicum nodosum* Kunth, as there seem to be all intergrades between the large- and small-panicled forms. The differences indicated by E. G. and A. Camus between *Hemigymnia arnottiana* Stapf and *H. multinodis* Stapf are wholly differences in size of the panicles and slight differences in the disposition of the spikelets, but these do not appear to me to be constant; there seem to be no differences in the size and details of the spikelets. Backer recognizes but a single species as occurring in Java, and I am of the opinion that he is correct. The differences in the size of the plants and of their panicles seem to be largely due to differences in habitat. The synonymy as I understand it is as follows:

Panicum nodosum Kunth Enum. 1: 97. 1833 (based on *Panicum multinode* Presl); Hook. f. Fl. Brit. Ind. 7: 43. 1897.

Panicum multinode Presl Rel. Haenk. 1: 303., 1828, non Lam.

Panicum violaceum Llanos Fragm. Pl. Filip. 42. 1851.

Panicum arnottianum Nees in Steud. Pl. Glum. 1: 59. 1854.

Panicum ouonbiense Balansa in Jour. de Bot. 4: 142. 1890.

Hemigymnia multinodis Stapf in Prain Fl. Trop. Afr. 9: 742. 1920; E. G. & A. Camus in Lecomte Fl. Gén. Indo-Chine 7: 454. 1922.

Hemigymnia arnottiana Stapf l. c., E. G. & A. Camus op. cit. 455.

Panicum malabaricum Merr. in Philip. Jour. Sci. Bot. 4: 248. 1909; Backer Handb.

Fl. Java 2: 159. 1928, non *Poa malabarica* Linn.

This species is widely distributed in tropical Africa, tropical Asia, Malaysia and the Philippines.

The form occurring in Kwangtung Province, China, and in Indo-China, is considered by Henrard to represent a species distinct from both *Panicum nodosum* Kunth and *P. arnottianum* Nees. It has somewhat smaller spikelets than these, which I consider to represent a single species, usually about 2 mm. long, but apparently varying from 1.5 mm. to 2.5 mm. in length. In *Panicum nodosum* Kunth (*P. arnottianum* Nees) they are 3 mm. long. The chief spikelet differences appear to be in the size, as the glume characters seem to be rather remarkably uniform. I do not recognize *Ottlochloa* (*Hemigymnia*) as generically distinct from *Panicum*, and, under the circumstances, prefer to retain Balansa's varietal name, rather than to propose a new binomial for the southeastern Asiatic form. *Panicum nodosum* Kunth var. *micranthum* Balansa is the form that is represented in the Linnaean herbarium by an Osbeck specimen from the vicinity of Canton named by Linnaeus *Poa malabarica*. The application of this specific name is discussed under *Diplachne malabarica* (Linn.) Merr. The synonymy of this small-spikeleted form is as follows:

- Panicum nodosum*** Kunth var. ***micranthum*** Balansa in Jour. de Bot. 4: 142. 1890.
Poa malabarica herb. Linn., non *Poa malabarica* Linn. Sp. Pl. 69. 1753.
Hemigymnia arnoltiana Stapf var. *micrantha* A. Camus in Lecomte Fl. Gén. Indo-Chine 7: 455. 1922.
Hemigymnia malabarica Henrard in Meded. Rijks Herb. Leiden 61: 12. 1930, non *Poa malabarica* Linn.
Ottochloa malabarica Dandy in Jour. Bot. 69: 54. 1931, non *Poa malabarica* Linn.
Panicum nodosum Hitchc. in Lingnan Sci. Jour. 7: 219. 1931, non Kunth.

A form only known from Kwangtung Province, China, and Indo-China.

Hooker f. (Fl. Brit. Ind. 7: 332. 1897) cites as a synonym of *Centotheca lappacea* Desv. "*P[oa] malabarica*, Linn. Sp. Pl. 69; Burm. Fl. Ind. 27, t. 11, f. 2," on the basis of which I erroneously transferred the above specific name to *Centotheca* as *C. malabarica* (Linn.) Merr. in 1906. Hooker's error was in the citation of the Linnaean reference, as *Poa malabarica* Linn. Sp. Pl. 69. 1753 has nothing to do with *Centotheca*, but *Poa malabarica* Burm. f. Fl. Ind. 27. pl. 11, f. 2. 1768, is clearly the same as *Centotheca lappacea* (Linn.) Desv. = *C. latifolia* (Osbeck) Trin. As the Linnaean binomial *Poa malabarica* has thus been erroneously associated with *Centotheca* it is briefly discussed here. No attempt has been made to compile the very numerous synonyms, of which Hooker f. cites no less than 22. Those given below are chiefly those necessary to explain the acceptance of the specific name *latifolia*, with several additions to Hooker's list. There are probably over 30 synonyms for this very common, characteristic, and widely distributed species.

Centotheca latifolia (Osbeck) Trin. Fund. Agrost. 141. 1820.

Holcus latifolius Osbeck Dagbok Ostind. Resa 247. 1757; Linn. Syst. ed. 10, 1305. 1759.

Poa latifolia Forst. f. Prodr. 8. 1786.

Poa malabarica Burm. f. Fl. Ind. 27. pl. 11, f. 2. 1768, non Linn.

Cenchrus lappaceus Linn. Sp. Pl. ed. 2, 1488. 1763.

Centotheca lappacea Desv. in Nuov. Bull. Soc. Philom. 2: 189. 1810.

Melica philippinensis Llanos Frag. Pl. Filip. 44. 1851.

Centotheca malabarica Merr. in Philip. Journ. Sci. Suppl. 1: 385. 1906; Koord. Exkursionsfl. Java 1: 159. 1911, non *Poa malabarica* Linn.

Anthoxanthum pulcherrimum Lour. Fl. Cochinch. 29. 1790.

It may be noted that Trinius in publishing the binomial *Centotheca latifolia* based it on *Cenchrus lappaceus* Linn.; "*Centotheca latifolia* (*Cenchrus lappaceus* L.)," but later (Mém. Acad. St. Petersb. Math. Phys. Nat. 1: 358. 1830) under *Uniola lappacea* Trin. = *Centotheca lappacea* Trin. = *C. latifolia* Trin., he cites *Holcus latifolius* Linn. as a synonym. Linnaeus in 1759 cites Osbeck's references but does not credit the binomial to Osbeck, yet Osbeck's binomial antedates Linnaeus' use of it by two years.

Sex and chromosomes in plants

CECIL YAMPOLSKY

(WITH 16 TEXT FIGURES)

If an increasing number of corroborative evidences is a measure of the validity of an assumption, then the existence of the sex chromosome in plants is an established fact and the problem of sex determination is no longer a problem from the Mendelian standpoint; it has been solved. Sex determination in plants involves merely an extension of the concept that explains sex in animals. Lindsay (1930) lists forty-three angiosperm forms in which heterochromosomes have been found and that does not include the eight hepatics in which heterochromosomes are present. Since then more forms have been added to the list.

Ever since Allen (1917) announced the presence of sex chromosomes in the hepatic *Sphaerocarpos Donnellii*, there has been a steady gain in the number of plants that are shown to have a correlation between sex expression and a specific chromosome. On the other hand, negative evidence, both among angiosperms and hepatics where no obvious correlation exists between sex forms and a special chromosome, has accumulated.

The cell concept held sway for three quarters of a century. In its time old values were brushed aside and new values established. Since the beginning of the twentieth century the supremacy of the cell in biologic thought has had a contender in the form of the newer genetics, Mendelism. Both the Galtonian and the Mendelian analyses of genetic phenomena are mathematical. They deal with populations and involve a statistical approach towards biologic problems. Parents and children are compared numerically; all morphological and physiological attributes of the organism are in reality conceived in terms of units and as numerical values even when the claim is made of a distinction between qualitative and quantitative characters. Hybrid and non-hybrid, heterozygous and homozygous! Sex has its explanation in the mating of a homozygous individual with a heterozygous individual. What clearer parallelism could have been conceived to account for the one to one ratio? Segregation of genes! A magic formula in which a series of complex phenomena find their simplification.

In recent years we have witnessed an alliance between a discipline like Mendelism with its mathematical ideology, a discipline where the unit one is not an individual but a number, and a discipline such as cytology which deals with actual individuals and more specifically with the ultimate units of the organism, the cells. From this alliance hybrid offspring have arisen, not with blended inheritance, but with conflicting developmental tendencies. At the present moment cytology accepts all the pro-

nouncements of the geneticist. When the mathematician-biologist gets into difficulties with his calculations the cytologist extricates him by directing his attention to the multiplicity of possible structural elements in the nucleus, viz. maternal and paternal chromosomes, serial arrangement of genes, chromatin granules in pairs, parasynapsis, chiasmotypy, four-strand crossing-over, non-disjunction, fragmentation of chromosomes, polyploids, diploids, triploids, tetraploids, and not to forget sex chromosomes or heterochromosomes, and bids him take his choice. Explanations come from one part of the cell—the nucleus, and particularly from a special part of the nucleus, the chromosome. What does a philosopher think of such a marriage of convenience between genetics and cytology? Truly an eclectic approach to the solution of the problem of life! The geneticist thinks in terms of summations and subtractions and arrives at his conclusions through the manipulation of irreducible non-visible entities, genes, and the cytologist, abandoning the building stone, the cell with its self-perpetuating organization, is led to interpret with greater and greater freedom the very difficult data as to the mating of colloidal germ plasms in terms of the additions and subtractions of genetical experimentation.

Alternative sex inheritance can be described in terms of heterochromosomes providing opposite sexes are in question. In the plant kingdom, dioecism is wide-spread but it is not the preponderant condition. The large array of sex forms in the phanerogamic flora should make one pause before postulating an all-embracing scheme to explain sex in plants. Hermaphrodite, dioecious, monoecious, andromonoecious, gynomonoecious, androdioecious, gynodioecious, polygamous, polyoecious, and combinations of the various groups give over forty sex categories in the flowering plants not including the quite independent but equally demonstrable data on compatibilities. If our knowledge of evolutionary trends were sufficiently sure to allow us to say with certainty that dioecism is a derived condition and is the most recent sex state, then we would be justified perhaps in correlating this separation of sexes with definite chromosomes in the gamete cells. A survey of the distribution of the sexes (Yampolsky, 1922) fails to show that dioecism is the end goal of sex expression in the various families. Neither the monocots nor the dicots show orthodox leanings towards any one sex category. The currents of sex differentiation in the families of plants may run parallel; they may cross; they may run upstream or down-stream. From the heights they look like a patchwork quilt of many hues and designs. Why should one sex form, dioecism, be correlated with the presence or absence of a particular chromosome? Is hermaphroditism less of a sex condition? What about monoecism and the other sex categories? Cytology has failed to yield evidence which would

tend to show a correlation between chromosome number, size, or form and phylogeny (Farmer and Digby, 1914). Why should dioecious plants have been singled out for such a correlation? Why should a quantitative difference in chromosomes effect morphological differences in males and females? Why should there not be a similar correlation in all forms of sex expressions? Why should some dioecious plants show no visible correlation? Certainly the change from a non-sexual sporophyte to one that produces eggs or sperms or both is sufficiently profound, since climax structures—flowers, are achieved. We have no such evidence. That changes in the germ plasm must have occurred no one can deny. We do not know how the modification in the protoplasm was brought about.

The presence of sex chromosomes in hepatics is not comparable with the presence of such bodies in flowering plants. In *Sphaerocarpos Donnellii*, *S. texanus*, *S. terrestris*, *Riella helicophylla*, *Pellia Fabbronia*, *P. Neesiana*, *Moerckia hibernica*, and in *Makinoa crista*, sex determination is associated with the reduction divisions. Sex is expressed when maternal and paternal hereditary complements separate. The union of sex chromosomes in the forms listed, results in a neutral sporophyte. That sporophyte contains x and y chromosomes and it exhibits no morphological expression correlated with those chromosomes. What becomes in this case of the concept that sex chromosomes operating in a common medium give rise to one or the other sex depending upon quantitative or qualitative equality or difference? If sex chromosomes have any significance in hepatics they suggest the fact that *sex expresses itself at the end of a cycle*. In these forms it is when cells throw off the yoke of duality that we have the fullest manifestation of sex. Fertilization yokes the two gametes and robs them of their independence.

The gametophyte expression in liverworts, in mosses, and in ferns is the expression of an independent haploid generation with but one set of chromosomes. On the assumption that sex chromosomes operate independently in such gametophytes there should be no possibility of sex reversal. In spite of Allen's (1932) pronouncement about the strict unisexuality in certain species of *Sphaerocarpos*, that the plants arising from the spores from the beginning are predestined to be male or female and no change in conditions may induce intersexuality or sex reversal, the case for obligate maleness or femaleness is weakened by his own statement that the genus *Marchantia* includes also hermaphrodite species.

Gertraud Haupt's work (1933) on *Marchantia grisea* has just appeared. It forms an important link in the chain of observations on the liverworts. This liverwort is androdioecious since only hermaphrodite and male plants exist. The male plant contains nine chromosomes, four paired ones

and one unpaired. The male sex organs of the hermaphrodite are borne on separate branches, so also are the female sex organs. Some branches contain both male and female elements. The cells of the hermaphrodite plant contain ten chromosomes. The female sex organs contain ten chromosomes, one a very small one called the *z* chromosome. The male sex organs on the hermaphrodite plant contain nine chromosomes. In the formation of the male sex organs the *z* chromosome is lost. Fertilization gives to the sporophyte nine and nine and one (*z*) chromosomes, nineteen in all. The *z* chromosome is responsible for the female sex; the unpaired chromosome is responsible for the male sex. In the sporophyte the two male chromosomes pair; the female sex chromosome alone remains unpaired.

The literature on intersexuality in liverworts is meager but as few as the cases may be they point to a fluidity of sex expression. Taylor (1836) described an androgynous gametophyte in *Dumortiera irrigua*. Townsend (1899) found archegonia on the male thallus of *Preissia commutata*. Ernst (1907) found androgynous receptacles in *Dumortiera velutina*. Cutting (1910) found antheridia on the archegoniophore of *Marchantia polymorpha*. Limpricht (1890) found intersexual stages in *Jungermannia Kaureni* and *Cephalozia Gottschei*.

In the dioecious mosses, in dioecious fern prothallia, and in heterosporous ferns mixed sexuality occurs (Yampolsky, 1919). Whatever the determining factors that produced gametophytes of one sex may have been, they are not absolute in their effects because transitions from one to the other sex have been observed.

Sphaerocarpos Donnellii (Allen, 1919) and *Riccia Curtisii* (MacAllister, 1928) show an interesting parallelism since the spores are held in tetrads and since also upon germination of those spores there appears to be an equal distribution of males and females. This would indicate a similarity in the mechanism of sex determination. A cytological examination of *Riccia* shows no such similarity.

Contrasting the hepatics with sex chromosomes reported with those in which no sex chromosomes have been observed we may well ask ourselves what the significance of the sex chromosome is. We cannot deny its presence but its absence does not suppress sex. In *Riccia*, in *Marchantia*, in *Conocephalum*, in *Riccardia*, in *Blasia*, in *Diplophyllum*, in *Scapania*, sex expression is as patent and as evident as in *Sphaerocarpos*, in *Riella*, in *Pellia*, in *Moerckia* and in *Makinoa*. There is no direct evidence that *x* and *y* chromosomes in hepatics control sex. If the *x* and *y* chromosomes have any significance in hepatics it is an indirect one; they are found to accompany sex but apparently not to control sex determination.

In approaching the problem of sex chromosomes in flowering plants it

is with the realization that the task is a difficult one. It was a foregone conclusion that when genetical data and chromosomes became interrelated in the minds of investigators, sex would find its explanation in chromosomal structure too. That such is the case is an accepted fact. The Mendelian concept of sex demonstrated in animals and accepted by students of sex in plants received its final support in the discovery of sex chromosomes in plants. And curiously enough its discovery in the liverworts complicated rather than clarified the situation. In the liverworts sex is determined at the reduction division; the plants resulting from the haploid spores do not have their counterpart in the animal kingdom. The gametes of the animal, egg and sperm, contain the sex chromosomes but those gametes are quite limited in their capacity for development; they have not the power of self-propagation; they die unless they mate. From such a mating individuals arise male and female; sex is determined at fertilization. Sex is determined when duality is established. In the liverworts and their like sex appears when duality is broken down. A comparable situation? Not at all! The explanation that holds for sex in the liverworts does not hold for sex in animals nor for sex in flowering plants. Sex in flowering plants it is claimed, is established at fertilization just as it is in animals and by the same kind of mechanism. A curious paradox! In the case of the liverworts, mosses and ferns, sex is established at reduction division. In the dioecious flowering plants the reduction division dissolves the sexual state. In liverworts fertilization results in a non-sexual sporophyte, and x and y chromosomes do not influence morphological expression. In flowering plants fertilization results in a sexual sporophyte and x and y chromosomes do influence morphological expression. There is no correlation between sex determination in flowering plants and sex determination in the liverworts. If sex chromosomes in dioecious flowering plants are determiners of sex the explanation must be sought in the parallel phenomenon in animals.

To deny the existence of bodies in the cell that behave differently from the mass of chromosomes would be not to believe what the eye sees. Such bodies are demonstrable and their behavior can be traced as much as behavior stages in coagulated protoplasm can be traced. Knowing the nature of the sex to be investigated and finding structures in the sex cells that lend support to digamety, it takes no subtle reasoning to correlate the two. The reasoning is as follows: paternal and maternal chromosomes pair, equal with equal, male chromosome with female chromosome. If male and female chromosomes differ in one or more respects, either from one another or from the autosomes, that difference will stand out when the two pair prior to reduction division.

Such cytological evidence would be unassailable if somewhat analogous

phenomena were not observed in hermaphrodite plants that undergo what is commonly called abnormal meiosis—whether the abnormality is due to physiological disturbances other than hybridity, or is due to disturbances in hybrids as a result of various incompatibilities. I have examined a large number of such cytological figures and it would have been easy to make out a case for gametic heterozygosity in many of them. I have before me the work of Sinoto (1929) in which he describes sex chromosomes. From the point of view of the classical cytologist, the inadequacy and the crudeness of the figures accompanying the observations would weaken the author's evidence. Yet it is accepted and quoted.

All the evidence to support sex and sex chromosomes is circumstantial. Is that not also true for the evidence that links cell form and function with chromosomes? Have not the defenders of the sanctity of the sex chromosomes begun to feel the need of accessory hypotheses? The reason is that the conception of sex as an alternative inheritance is untenable. Intersexualism is no longer the game of the teratologist. It is a widespread condition. The intersexual forms bridge the gap between male and female. But where are the bridging chromosomes between x and y ?

It is an obvious fallacy to predicate that a part is greater than the whole. Yet in practice, cytology has subscribed to that principle. And the greatest supporters of that fallacy have been those who have read into the chromosomes all the characteristics of the adult individual. At best cytological evidence is circumstantial. The technique that the student of the cell has evolved yields him clues from which he may reconstruct physiological processes. The very stages in mitotic division of which we have but an incomplete knowledge are but the parts of a chain visible to the eye. We then reconstruct in our mind the steps that cannot be seen. When a cell is activated towards division we cannot visualize the urge. Yet that 'urge' makes itself felt in all parts of the cell; in the cell wall, in the cytoplasm, and in the nucleus. Our attention has been focused upon the activities of a part of the nucleus and the dramatic qualities of the performers have made us forget the silent forces that pull the strings that make the actors act. The pattern of nuclear and cell division is universal, the discrete bodies, chromosomes, move through space, now they are together, now they are separated perhaps to continue their activities. The chromosomes, visible to the eye, have caught the fancy of the world; the actors make the play.

The sex chromosome has been singled out for an especially important rôle and to it are attributed far-reaching properties. If we take such a chromosome and place it side by side with the morphological and physiological characteristics bound up with a particular sex, sex-linked, we say,

we find strange contrasts. The sex-chromosome may be directly responsible for the primary and secondary sex expressions. I have examined the chromosomes in the male plant of *Mercurialis annua* (Yampolsky, 1925) and I have followed some of the steps from the undifferentiated pollen mother cells to the tetrads where the final distribution of chromosomal material has been achieved. And from those observations I was unable to single out a chromosome which seemed to bear the burden of sex determination. I found no correlation between one chromosome and the distinguishing characteristics of the male plant. Granting for the moment that one of the eight chromosomes is a sex chromosome and granting also for the moment that the male plant possesses secondary sex characters, we can diagram the relationship between the sex chromosomes and the visible secondary sex characters thus:

Sex chromosome responsible for:	{	inflorescence—spike
		color of plant—light green
		leaves—longer than in female
		petiole—longer than in female
		internodes—longer than in female
		angle of branching— 45° —a lesser angle than in female
		branches—less ramified than in female
		growth—less vigorous than female
	individual flower {	calyx { anther, pollen grains
		stamens { filament

What holds true for the male determining chromosome must equally hold true for the sex chromosome and secondary sex characters in the female, thus:

Sex chromosomes in the female responsible for:	{	inflorescence—sessile
		color of plant—dark green
		leaves—shorter than in male
		petiole—shorter than in male
		internodes—shorter than in male
		angle of branching— 90° —greater than in male
		branches—more ramified than in male
		growth—more vigorous than in male
	individual flowers {	calyx
		ovary
		ovule
		stigma
		style
		embryo sac

The other characteristics of the plant, male or female, owe their expression to the so-called autosomes. The absence of a definite correlation

between any one chromosome and morphological expression became apparent from a study of the characters that are sex limited. The evidence gathered (Yampolsky, 1930) shows that all the characteristics of one sex may have their counterpart in the plant of the opposite sex; that leaf, petiole, internodes, angle of branching, vigor of growth, etc., do not behave as units but show a great range of variability grading from one extreme into the other. Sex intergradation in *Mercurialis annua* is widespread without attendant sterility. We have then the curious condition of one side of an equation which is constant being equal to the other side which is variable. The equation in which a sex chromosome in the male gamete is responsible for, or is equal to, primary and secondary sex characteristics is no longer an equation when the variability of one side is not counterbalanced by an equal variability in the sex chromosome. But, those who describe sex chromosomes recognize them because of their constancy and do not claim variability for them. Variability in sex expression previously considered sex-linked has now been explained in terms of autosomal influences.

The fact nevertheless remains that sex in dioecious plants is explained on the assumption that one of the parents is heterozygous for sex and consequently, there are either two kinds of sperms or two kinds of eggs. That has been the explanation which has gained almost universal acceptance. And the proof? Cytological evidence of gamete dimorphism and experimental evidence of the more or less one to one ratio of males and females. It seems like a logical and unassailable explanation.

Mercurialis annua is unique among experimental plants inasmuch as it can be used to test out the validity of the assumption that one or the other of the sexes is heterozygous for sex. Isolated male plants produce seeds and such seed when germinated gives rise to male plants only. The importance of that phenomenon cannot be overemphasized since the male plant without the intervention of the female plant registers its genetic constitution. How does it do it? It produces its own embryo sac with an egg apparatus. It produces pollen grains. Pollination takes place followed by fertilization and embryo formation. If males are heterozygous then two kinds of pollen grains should be produced and therefore two kinds of offspring male and female. But all the offspring of all the males that produce seed are male (Yampolsky, 1919).

Isolated female plants produce seed and such seed when germinated give rise to female plants only. The female plant without the intervention of the male plant registers its genetic constitution. How does it do it? It produces its own pollen grains with their generative cells. Pollination takes place followed by fertilization and embryo formation. If females are hetero-

zygous then two kinds of offspring should be produced, male and female. But all the offspring of all the females that produce seed are females (Yampolsky, 1919).

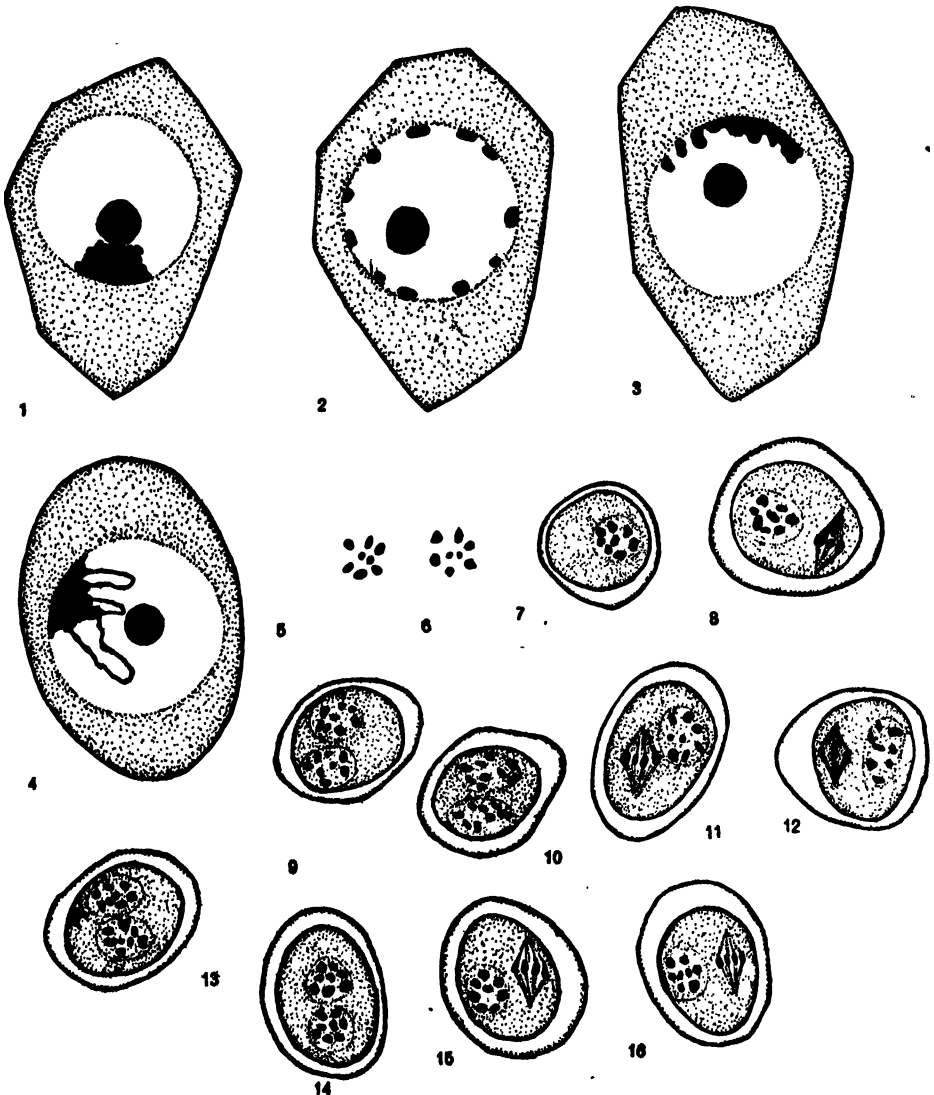
The pollination of female plants by male plants results in seed that produce male and female offspring. Cytologic and genetic evidence obtained from *Mercurialis annua* does not lend any support to the conception of gametic dimorphism. Are we to regard that plant as a non-conformist and therefore outside the pale of consideration? On the contrary, its possibilities should be exploited to the fullest extent. If selfed males and females can be obtained in *Rumex*, in *Lychnis*, in *Humulus*, in *Elodea* and the other plant forms for which it is claimed that sex-chromosomes are present, they should be tested out.

Until a direct relationship can be established between chromosomes and form and function we are not justified in ascribing particulate inheritance to the chromosomes. In spite of our advances in the study we cannot say with any degree of finality that chromosomes bring about definite morphological expressions. Why is it not just as tenable to say that chromosome form and number constancy are expressions of the cell's activity. The cytogeneticist forgets that between the initiation of the steps that result in a two-celled embryo and all the countless divisions that result in a highly complex plant other forces have intervened. He forgets that differentiation may also be a matter of spatial distribution of cells. A dividing cambium cell does not predetermine which of its two daughter cells is to be xylem, which is to be phloem. Position alone appears to determine that. In the mature individual cell adjustment, tissue adjustment, and organ adjustment, take place. Cells and organs undergo environmental changes. Two cells isolated are environmentally different from two cells exerting pressure upon one another. Many cells in contact are in an even more modified environment.

To look at a gamete cell with its chromosome complement—a cell that has been fixed and stained, all of whose parts have been congealed into inaction and to read therefrom the profound processes of development is a too great simplification of a yet only partly solved problem. We persist in saying that a part is greater than the whole.

The polygamous plants of *Mercurialis annua* bridge the gap between males and females. These intersexual forms show a graded series between males and females. I have pointed out (Yampolsky, 1930) that intersexualism expresses itself in any part of the plant and in varying degrees. Aside from the appearance simultaneously of male, female, and hermaphrodite flowers, polygamous forms may also produce modified male inflorescences. This study concerns itself with the cytology of male flowers on poly-

gamous forms. Lest there be any doubt as to the nature of the sex of the plants examined it must be emphasized that all polygamous forms start out as females and produce female flowers exclusively over a period of



Figs. 1-16. See text for explanation.

months. In the forms under observation not a single male or hermaphrodite flower was produced from May until July. After that sporadic male and hermaphrodite flowers appeared and as the plants grew in vegetative vigor, the increase in the numbers of males and hermaphrodites was ac-

celerated. Male branches and individual male flowers were fixed in Flemings medium solution and stained with safranin and gentian-violet and orange G. At the same time male branches from male plants were also fixed and stained. For comparative material the prepared slides used for the study of male flowers (Yampolsky, 1925) were also examined.

All the conventional maturation stages that were observed in purely male material were found in the male flowers taken from the polygamous forms. During synapsis the pollen mother cells with their polygonal outlines show a very densely staining cytoplasm. The nuclear material is aggregated to one side—nucleolus and chromatin material are in a close snarl. The red stain of the nucleolus differentiates it from the massed chromatin. The pollen mother cell nuclei with the material heaped up on the periphery of the nuclear membrane, showed a definite orientation and raised the question whether that stage has its counterpart in the uninjured living cell. We forget that living matter fixed, is no longer living matter. Congealed water forms definite patterns from which we can deduce certain physical principles which do not necessarily hold for water in the liquid state. Protoplasm, a labile substance, subjected to the congealing properties of the fixing fluid, gives us a picture of dead irreversible protoplasm. Text figure 1 illustrates the degree of chromatic aggregation in the pollen mother cells. The massed material originates from the pro-chromosomes which in *Mercurialis annua* are arranged on the periphery of the nuclear membrane (fig. 2). In figure 3 several of the pro-chromosomes can be distinguished while others have passed into an amorphous state.

When the pollen mother cells have separated from one another and have rounded up, the chromatic material is no longer clumped but appears in the form of loops or threads. *Mercurialis annua* yields no good evidence either for parasynapsis or telosynapsis. As a matter of fact the significance of those stages, if they have any significance, is obscure. The conspicuous change is in the rounding up of the cell as a whole (fig. 4). Whatever physiological processes go on in the anther they bring about a separation of cells.

The preparations for reduction division in an already delimited sporophyll indicate a sexual segregation, physiological and morphological, long before the actual reductive stages. The steps leading towards the final division of the spore mother cell must be conceived as the fundamental ones in the long chain of sex expression that results in the production of gametes. If we could penetrate into the meaning of sexuality we could better understand the phenomenon known as meiosis. The newest meaning of sex, fresh from the pen of Darlington (1932) is nothing more than an amplification of Darwin's idea that hybridization increases variability. Darlington

is firmly convinced that pairing of chromosomes, maternal and paternal, occurs at meiosis and subsequent splitting results in a four strand chiasma. Under such conditions interchange of chromosomal segments can take place and does take place. Sexuality has no virtue save that it offers an opportunity for gene interchange, a crossing over, that results in variability. Meiosis has a justification; it encourages hybridity. Darlington, in common with many others, assumes that interchange of chromatic material takes place in the nucleus at meiosis only. The direct evidence for chiasmata, in spite of Jannsen's newest work (1924), is not convincing. Yet its theoretic value for genetic interpretations has been used with unusual effect in explaining genetic phenomena. If we admit the compact knot in synapsis then we must admit that whatever individuality chromosomes have had before entering a fusion stage, must have been lost in that stage. So intimate a mingling of nuclear material, must from the nature of the physical state of protoplasm, result in an exchange of material, not that exchange would necessarily mean a realignment of genetic entities. It seems inadmissible to infer that chromosomes resolved into chromatin and linin in intimate juxtaposition in the so-called resting stage could separate wholly uncontaminated. The debate between Sax (1932) and Darlington (1931) on chiasmata, in view of our inadequate knowledge of that phenomenon becomes an academic question of what would happen if one set of premises were correct and the other wrong.

The nucleolus during the meiotic stages becomes very conspicuous and even though it does not go through the complicated steps in division, its increase in size is an evidence that it is associated with active physiological processes. What these processes are I am not prepared to say. Because the nucleolus does not divide equationally is no indication that it is not concerned in the transmission of genetic properties. The extra nuclear nucleoles scattered through the cytoplasm during heterotypic division become an important part of the picture, even though we may have failed to find a particular function for the fragments. We have been so greatly impressed by what appears as an equational division of the chromatic material, that the rest of the cell becomes subordinate in our minds. No matter how thoroughly we trace back the units of heredity, and we have become satisfied that they have no accomplices, we can never get them to act alone. The chromosomes of the egg nucleus are in the cytoplasm of the embryo-sac from which they cannot escape. The sperm nuclei in the pollen tube are surrounded by the cytoplasm of the pollen grain. When they are discharged into the embryo-sac the cytoplasm is discharged with them. In hereditary transmission in the flowering plants, two cell complexes are concerned and whatever cytoplasmic properties the gamete cells have in

common with the adult from which they originate, they must be conceived as hereditary transmissions in as true a sense as are the 'Anlagen' which are presumed to reside in the chromosomes. A plastid from an egg of *Fucus*, an integral part of the female gamete, must be considered as evidence for the passing on of hereditary characteristics through the agency of the cytoplasm. Until we can definitely prove that the nucleolus which in *Mercurialis* exhibits marked increase in size during the maturation division in both the macro and microsporogenesis and beyond is useless, we must accept it as an integral part of genetic continuity. The specificity of protoplasm is, as we know, not limited to the nucleus. The study of blood relationships in animal forms must act as a reminder to us that other parts of the cell are concerned in determining whether the germ nuclei may be allowed to pair. Compatibilities and incompatibilities among flowering plants indicate to us that barriers may be let down or set up depending upon the specificities of the cytoplasm.

In discussing the heterotypic division in the male plant of *Mercurialis annua* (Yampolsky, 1925) I stated that differences in chromosome shape and form occur but no chromosome behaves in a manner which would point it out as different from any other. I have never understood the reasoning as to why a sex chromosome should behave differently from any other chromosome during division. Nor am I able to understand why a chromosome that lags behind during the division stages is necessarily identified with sex tendencies. Unpaired chromosomes in crosses involving the mating of two forms differing in chromosome number show such aberrant behavior and certainly no one would consider this behavior as having anything to do with sex. In *Mercurialis annua* the chromosomal variations do not warrant the assumption that chromosomal differences of distinct male and female quality are present. It is in the homeotypic division, that the variations in chromosome size and form appear most pronounced. Just as in the male, so too in the polygamous form, the homeotypic chromosomes in many of the polar views show two smaller chromosomes surrounded by six larger ones (figs. 5 and 6). That this is but a chance arrangement becomes evident from the study of a large number of polar views. The position of the chromosomes in relation to one another can have no significance since they are but transitory stages in a long process which results in the formation of the pollen grains. At this stage too the first outlines of what is to be the region of the nuclear membrane can be seen because of the difference between the density of the cytoplasm around the chromosomes and the rest of the cytoplasm.

The condition of pairing of chromosomes is most commonly met with in the diploid organism and particularly during the maturation phenomena.

In the haploid condition in *Mercurialis annua* pairing occurs, usually between chromosomes of equal size. Figures 7, 8, 9, 10 male and polygamous plants, show such pairing. The observations are of interest because they do not involve any of the theoretical requirements as to pairing. The chromosomes do not maintain constancy in size nor in form. Without actually measuring the chromosomes it can be seen that the total mass represented by a group of eight chromosomes may be equal to, may be less, may be greater than, that of a neighboring set of eight chromosomes. The chromosomes may be ovoid, spherical, or irregularly polygonal in outline, their edges may be rough or smooth. Figures 7 to 16 taken from male and polygamous plants show similarity in the life history of the two gametes. What has already been said for the nuclear figures of the male plant (Yampolsky, 1925) can be said for the nuclear figures in the male flowers on the polygamous plants.

The quest for sex chromosomes has led to their discovery in unexpected places. The breeding experiments of Shull (1914) between the phenotypic hermaphrodite *Lychnis* and the dioecious female lead him to conclude that some of the hermaphrodites were really genetic males. Shull's hypothesis finds a beautiful substantiation in Belar's (1927) cytological investigation of that form. Genetically and cytologically the hermaphrodite is not an hermaphrodite; it is a male with conspicuous x and y chromosomes present in both the male and female elements of the flowers.

Miss Pastrana (1932) reports an unusual mode of sex determination in *Begonia Schmidiana*. The sporophyte chromosome number in that form is thirteen—six paired chromosomes and one unpaired chromosome. The unpaired chromosome has to do with sex determination. The female flower of the monoecious plant has thirteen chromosomes; the male flower has twelve chromosomes. The unpaired chromosome fails to enter the stem initial from which the male flower develops. Consequently only one kind of pollen grain is produced—one with six chromosomes. In the reduction division that goes to form the megaspore, the unpaired chromosome goes undivided to one pole and the embryo sac arises from a nucleus with seven chromosomes.

In *Lychnis* form and function do not necessarily agree. A phenotypic hermaphrodite with its hermaphrodite flowers having stamen and pistil, is a genotypic male. What is the significance of the external expression of that plant? Of no significance! Where does maleness reside? In the gametes! The gametes alone express the sex of the plant since the phenotypic expression does not parallel the genotypic constitution of the plant. Male and female elements in the hermaphrodite flower mean nothing. The plants are only apparent hermaphrodites in reality they are males. One

may very well ask the question: "What determines the hermaphrodite expression?"

I must recall Correns' (1907) and Bateson's (1909) classic examples of crosses between *Bryonia dioica* and the monoecious *Bryonia alba* which resulted in the production of male and female sterile hybrids, recognized by their external appearance, an instance where morphology not physiology is used for sex identification. From these results Correns concluded that male *Bryonia dioica* was heterozygous for sex and Bateson from the same results concluded that the female *Bryonia dioica* was heterozygous for sex. What is the significance of the outward expression of sex? Of great significance! Where do maleness and femaleness reside? In male and female expressions in the sporophyte. What about the gamete? There are no gametes, the plants are sterile. Male and female elements are expressed by sterile male and female flowers. If those plants could be made to express themselves the male would be heterozygous—Correns; homozygous—Bateson; the female would be homozygous—Correns; heterozygous—Bateson. In appearance they are males and females; in reality they are non-entities, not even neuters.

Miss Pastrana's observations raise a number of questions. She herself says that the loss of a chromosome immediately presupposes a somatic reduction division which is later followed by a true reduction division. The germination of the macrospore with seven chromosomes to form the embryo-sac implies a selective mortality. What forces determine which cells are to be sacrificed? Such an assumption embodies a sex determining force independent of the one that regulates the differentiation of embryo sac mother cell tissue from pollen mother cell tissue. The contentions of Miss Pastrana would have been strengthened if she had succeeded in showing the fate of the chromosome that failed to enter the stem initial from which the male flower developed. In connection with these observations I wish to call attention to Sandt's (1921) work on *Begonia tuberhybrida*. He found pistillody present. An anther sac filled with pollen grains shows at its apex an embryo sac. If a male flower becomes so because of the loss of a chromosome how can it produce a structure with one chromosome more than it possesses?

In *Begonia Schmidtiana* somatic reduction occurs and is later followed by the so-called true reduction division. This new evidence is entered in the ledger, on the credit side of sex chromosomes. Nevertheless a curious paradox does exist. In dioecious flowering plants sex is determined at fertilization; in dioecious flowering plants, x and x or x and y determine sex; in dioecious liverworts it is x or y that determines sex. In the monoecious *Begonia* female sex is determined when x and y unite; the male sex is de-

terminated at the end of a cycle when the sporophyte loses a chromosome. In the monoecious (hermaphrodite) *Marchantia* femaleness is determined at reduction division in the formation of the spore and maleness is determined during the production of male sex organs when a chromosome is lost. How can we reconcile these divergent claims? As long as we shall ascribe to chromosomes the importance in heredity that we do, we shall see in chromosomal behavior all that we expect to see.

It is my opinion that in our desire to explore the world for new discoveries we often take painted scenery along so that when we come to barren wastes we can have the similitude of tropical scenery. We carry our categories with us. Sex falls into certain categories. Categories are man made. To classify, to label, to place into definite compartments biologic units that apparently belong together, is decidedly a human trait. The terms male and female connote circumscribed biologic units, units that have very close resemblances as well as very striking differences. Impressed by the differences we fail to detect the very fine gradations that exist, gradations which may insensibly bridge the differences that are conspicuous to the eye. Nineteen years of observation on *Mercurialis annua* have convinced me that obligate males and obligate females are but the extremes of a variable series. The *n*-numbers of sex forms refuse to submit themselves to the concept that sex is an alternative kind of inheritance. Neither sex categories nor sex chromosomes hem in the variability of sex expression exhibited by *Mercurialis annua*.

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Spathuliformae, a new section of *Codonanthe*

LYMAN B. SMITH

(WITH FIGURES 1-6)

In the process of studying some of Professor I. W. Bailey's collections from British Guiana, I came upon a peculiar specimen of *Gesneriaceae* which he had tentatively labelled as *Codonanthe*. The anthers had the irregular dehiscence and broad connective (fig. 3) which distinguish *Codonanthe* from the remainder of the family, but the filaments were fused into a broad ribbon attached to the ventral portion of the corolla-tube and the calyx consisted of but two lobes of very unequal size. Since all known species of *Codonanthe* had five-parted calyces and were supposed to have free filaments,¹ I at first supposed that Professor Bailey's material constituted a new genus.

However, a careful dissection of material of *Codonanthe cornuta*, *C. Hookerii* and *C. gracilis* soon demonstrated that, contrary to expectation, the filaments were fused although quite inconspicuously in the case of *C. Hookerii*. Also I noted that *C. cornuta* closely resembled the material in question in all but the form of the calyx, which was intermediate between the two-lobed type and the equally five-lobed type of *C. gracilis*, the type species of the genus. In *C. cornuta* the calyx is deeply cleft on each side of the dorsal lobe and much less between the four ventral lobes. This is evidently what Miquel referred to when he described the calyx as "spathaceo-fissus."² The failure of the filament character and the transition shown between the five-lobed and two-lobed calyces demonstrate that Professor Bailey's material belongs in the genus *Codonanthe*, but at the same time it is obvious that the genus is composed of two distinct sections as follows:

Eucodonanthe, calyce aequaliter 5-partito: corollae tubo amplo, basi postice gibbo: filamentis basi in vaginam brevem connatis. *C. gracilis*, species typica.

Spathuliformae, sect. nov., calyce distincte inaequaliterque bipartito, parte ventrali majori, spathuliformi, plus minusve 4-partita vel integra: corollae tubo gracili, basi postice calcarato: filamentis basi in vaginam elongatam connatis. *C. calcarata*, species typica.

Professor Bailey's material is then a new species of the section *Spathuliformae* and may be characterized as follows:

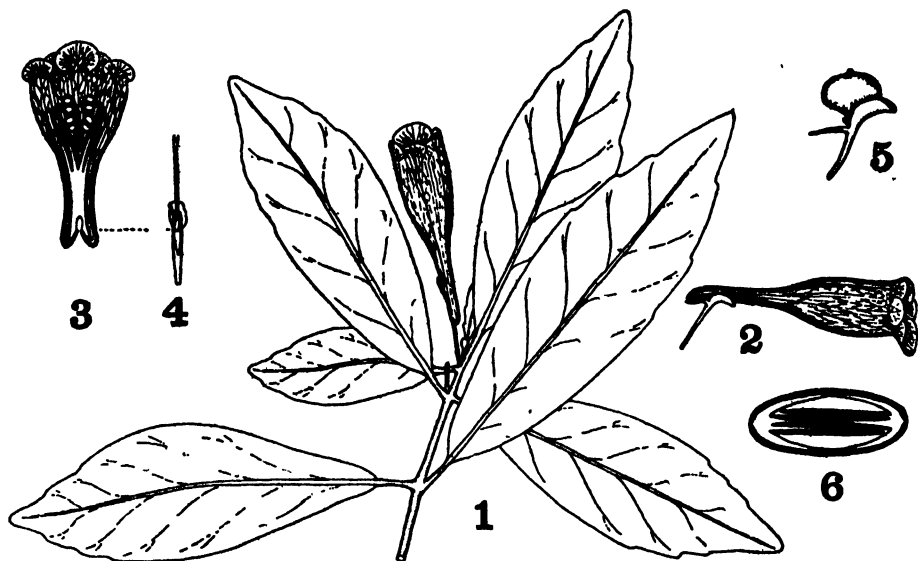
Codonanthe bipartita, spec. nov., caule elongato, ramoso, glabro: foliis oppositis, subtenuibus, glabris, ad 8 cm. longis, late oblanceolatis, integris vel

¹ Fritsch in Engl. & Prantl, Nat. Pflanzenf. 4: Abt. 3 b: 171. 1894.

² *Nematanthus calcaratus* Miquel in Linnaea, 22: 473. 1849.

ad apicem versus grosse sinuoso-dentatis, 5 mm. petiolatis: floribus axillaribus, graciliter pedicellatis; calyce inaequaliter bipartito, parte dorsali anguste lanceolata, parte ventrali integra, oblonga, obtusa; corolla alba, sicca aurea, 25–30 mm. longa, basi anguste tubulosa et calcarata, tum ampliata, infundibuliformi-campanulata, limbo patenti, 5-loba; staminum filamentis basi in vaginam elongatam connatis: fructu baccato, valde lateraliter compresso. Figures 1–6.

BRITISH GUIANA: Kartabo region, 1920, *I. W. Bailey 181* (type); same, *I. W. Bailey 110*. The following numbers appear to be conspecific: Waini River, Northwest District, lat. 8° 20' N., long. 59° 40' W., 1923,



Figs. 1–6.

CODONANTHE BIPARTITA L. B. Smith

1. Branch $\times 1$. 2. Lateral view of flower $\times 1$. 3. Corolla cut dorsally and laid open $\times 1$. 4. Calyx and pistil, showing dorsal gland, $\times 1$. 5. Calyx and fruit $\times 2$. 6. Enlarged diagrammatic cross-section of fruit.

De La Cruz 3735; upper Mazaruni River, long. about 60° 10' W., 1922, *De La Cruz 2294*.

Codonanthe bipartita is quite easily recognizable even in fruiting condition on account of its peculiar calyx. In addition the elongate seeds all lie parallel, as indicated in figure 6, and thus cause the soft fruit to assume a strong lateral compression.

INDEX TO AMERICAN BOTANICAL LITERATURE

1931-1933

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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